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SHOOT MORPHOLOGY IN THE *CLAYTONIA SIBIRICA* COMPLEX (PORTULACACEAE)

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ABSTRACT

The *Claytonia sibirica* complex, including *C. sibirica* and *C. palustris*, exhibits considerable morphological variation that encompasses ecological diversity over a wide geographic range. Shoots are basically rhizomatous in the complex and least specialized in *C. sibirica* var. *sibirica*. *Claytonia sibirica* var. *bulbillifera*, a serpentine endemic of southern Oregon and northern California, forms succulent, storage scale leaves distal to its foliage leaves each growing season. These scale leaves, which consist primarily of leaf base, are generally lacking in other members of the sibirica complex and give the shoot systems of *C. sibirica* var. *bulbillifera* a bulb morphology. *Claytonia palustris*, like *C. sibirica* var. *sibirica*, forms an apically swollen rhizome, but differs in its habit by forming renewal shoots, born in the axils of the basal leaves, at the ends of plagiotropic, single long internodes.

Key Words: Bulb, homology, leaf specializations, perennation, shoot architecture, serpentine.

The *Claytonia sibirica* L. complex consists of understory herbs of coastal and mesic inland forests extending from northern Santa Cruz County, California, to coastal northeastern Siberia (Miller et al. 1984; Chambers 1993; Miller 2003). The *C. sibirica* complex consists of annuals and perennials that exhibit considerable morphological, ecological and cytological variation over its range. Shoot systems in the *C. sibirica* complex have been most often described as rhizomatous, although shoot system specializations associated with geographic and ploidy variation have been described.

In the Klamath region (KR) of northwestern California and southwestern Oregon, *C. sibirica* have specialized underground structures involved in perennation (Gray 1877, 1887; Miller et al. 1884). Gray (1877) first described this KR form as *C. bulbifera* Gray and suggested it resembled *C. sibirica* but produced densely crowded perennating bulbs in a basal rosette. However, Gray's (1887) revision of the North American Portulacaceae treated *C. bulbifera* as *C. sibirica* L. var. *bulbillifera* Gray and described it as "...only a form of *C. sibirica* with thickened bases of the radical leaves, which persist on the crown as bulblet-scales."

Miller et al. (1984, p. 266) suggested that the *C. sibirica* complex consists of three basic morphotypes that differ in "shape of basal leaves and the presence or absence of basal bulblets and rhizomes". Gray's (1877, 1887) *C. sibirica* var. *bulbillifera* represents one morphotype recognized by Miller et al. (1984), which they characterize as bulbiferous, distinguished by elliptical basal leaves, and geographically localized to southern Oregon and northern California where it occurs frequently on serpentine substrates (Fig. 1). We will use this name to refer to the specialized KR morphotype. A second morphotype recognized by Miller et al. (1984) is found in shaded mesic habitats and has the deltoid basal leaf shape of

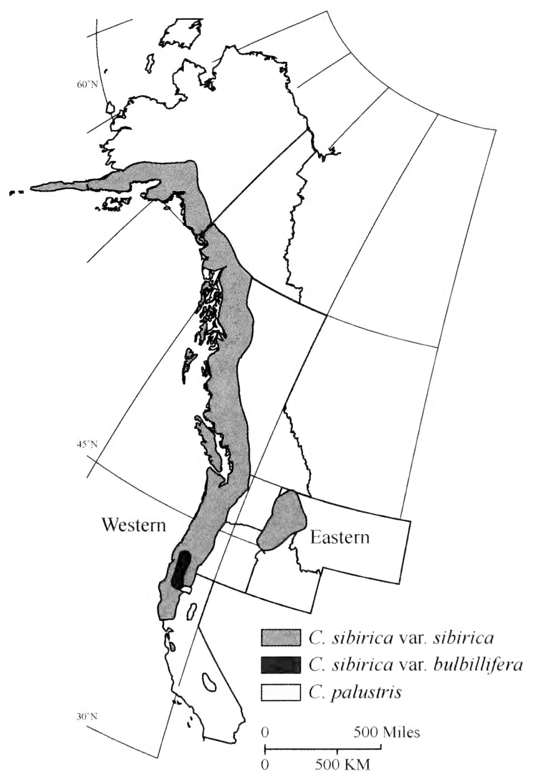

FIG. 1. Geographic distribution of the *Claytonia sibirica* complex.

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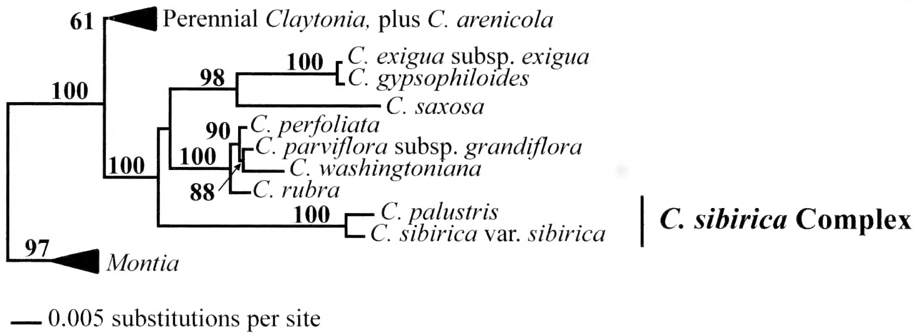

FIG. 2. Maximum likelihood cladogram from combined ITS and *trnK/matK* data showing phylogenetic relationships of the *Claytonia sibirica* complex from O'Quinn and Hufford (2005).

the type specimen for *C. sibirica* var. *sibirica*. We apply the name *C. sibirica* var. *sibirica* to populations distributed in the Pacific Northwest along the Cascadian cordillera, the Columbia River Gorge, coast ranges northward from Santa Cruz county, California, to Alaska, and the Aleutian and Commander Islands (Fig. 1). It overlaps with *C. sibirica* var. *bulbillifera* in the KR (Fig. 1). *Claytonia sibirica* var. *sibirica* also has disjunct populations in the inland Northwest (northern Idaho, western Montana and surrounding portions of Oregon and British Columbia; Fig. 1). We distinguish the morphological variation in *C. sibirica* var. *sibirica* as western and eastern morphotypes. Miller et al. (1984) characterized *C. sibirica* var. *sibirica* as bulbiferous also, but less so than the endemic KR morphotype (=*C.sibirica* var. *bulbillifera sensu* Gray 1887). The disjunct eastern populations of *C. sibirica* var. *sibirica* are reported to lack swollen leaves. The third morphotype discussed by Miller et al. (1984) was later described as *C. palustris* by Swanson and Kelley (1987). *Claytonia palustris* is narrowly endemic to two small, mid-elevation regions at the northern and southern ends of the Sierra Nevada and in Siskyou County, California, where it overlaps with *C. sibirica* var. *bulbillifera* at the eastern edge of its range (Fig. 1). This taxon is unique in the complex in preferring perennially wet, sunny habitats and was described by Swanson and Kelley (1987) as being strongly stoloniferous.

O'Quinn and Hufford (2005) found robust support for the monophyly of the Miller et al. (1984) *C. sibirica* complex based on plastid and nuclear ribosomal DNA sequence data (Fig. 2). Notably, all members of the complex share a unique 10 base pair motif that includes a three-base pair insertion in the internal transcribed spacer region of the nuclear ribosomal DNA. Phylogenetic results recovered a sister taxon relationship between *C. palustris* and *C. sibirica*, but lineages within *C. sibirica* were not resolved.

In this study we characterize shoot morphology of the *C. sibirica* complex, with a particular emphasis on specializations for nutrient storage and perennation. Beyond Gray's (1877) initial description of *C. sibirica* var. *bulbillifera*, the morphology of the so-called bulbiferous morphotype of the KR populations has not been studied previously. This comparative study of the shoot systems in the *C. sibirica* complex addresses especially the morphological identity of structures described as bulbs and bulbiferous and presents hypotheses for the origins of morphological specializations.

MATERIALS AND METHODS

We sampled specimens of the western morphotype of *C. sibirica* var. *sibirica* from the Williamette Valley, Columbia River Gorge and foothills of the Hood River valley, and of the eastern morphotype from the Lochsa and Clearwater River valleys (Table 1). *Claytonia sibirica* var. *bulbillifera* was collected in the Illinois and Rogue River valleys of southern Oregon where this variety is the most common morphotype (Table 1). Samples of *C. palustris* were collected at the type locality at Jones Creek in Butte County, California, and seeds for greenhouse grown material were collected from a population at Stubbs Lake, Butte County, California (Table 1). Based on the cytogeographic results of Miller et al. (1984), we assume that our collections of the eastern morphotype of *C. sibirica* var. *sibirica*, *C. sibirica* var. *bulbillifera*, and *C. palustris* are diploid. Collections of the western morphotype of *C. sibirica* var. *sibirica* are potentially either diploid or tetraploid. Miller et al. (1984) suggested that diploids and polyploids have the same shoot morphologies.

Comparisons of shoot system morphology for the four perennial forms of *C. sibirica* used scanning electron (SEM), and light (LM) microscopy. Specimens from natural, greenhouse and common garden populations were sampled in May or June and August (Table 1) for fixation in formalin-acetic acid (FAA). Specimens for SEM were dehydrated in a graded ethanol series, critical-point dried, and mounted on aluminum stubs prior to gold coating. We examined 5–8

TABLE 1. COLLECTION DATA FOR SAMPLED POPULATIONS OF THE *C. SIBRIRICA* COMPLEX. All vouchers are at WS.

Taxon name	Population location	Collection voucher	Collection date
Claytonia sibirica var. *sibirica* Eastern morphotype	Lochsa River sites:		
	Glade Creek	R. O'Quinn 483	17 May 2002
	Eagle Summit	R. O'Quinn 488	17 May 2002
	Ashpile Creek	R. O'Quinn s.n	25 Aug 2002
Claytonia sibirica var. *sibirica* Western morphotype	Columbia River sites:		
	Herman Creek	R. O'Quinn 492	20 May 2002
		R. O'Quinn 528	19 March 2003
	Bridal Veil Falls	J. Schenk 774	28 June 2004
	Hood River site:		
	Pine Mountain Road	R. O'Quinn 490	20 May 2002
		R. O'Quinn s.n.	31 Aug 2002
		R. O'Quinn 529	19 Mar 2003
		J. Schenk 774	28 June 2004
	Willamette River site:		
	Corvallis, OR	J. Schenk 773	27 June 2004
Claytonia sibirica var. *bulbillifera*	Southern Oregon sites:		
	Davis Creek	R. O'Quinn 494	22 May 2002
	Brigg's Valley Road	R. O'Quinn 504	23 May 2002
	Cave's Camp Road	R. O'Quinn 365	29 May 2001
		R. O'Quinn 474	05 Aug 2001
	Eight Dollar Mtn. Road	R. O'Quinn 290	24 May 2000
		R. O'Quinn 508	24 May 2002
Claytonia palustris	Northern California sites:		
	Jonesville (type location)	R. O'Quinn 330	4 June 2000
	Stubb's Lake (seed source for greenhouse grown collections)	C. Björk 5704b	Multiple collections between 2001 and 2004

individuals per morphotype for SEM. Specimens were examined at an accelerating voltage of 15–20 kV. Images were captured digitally using the program Quartz PCI (Quartz Imaging Corp. 1993–1998). Specimens for LM were dehydrated in a graded tertiary-butyl alcohol series (Johansen 1940), infiltrated and embedded in Paraplast™, sectioned at 16 μm, mounted on glass slides, stained with safranin-O and fast green, and examined with a Leitz light microscope. Microtomed sections were photographed or drawn using a drawing tube. To characterize shoot architecture and leaf base shape over ontogeny, we made cross and longitudinal sections through the basal rosettes of 3–5 individuals per examined population (Table 1) of western and eastern *C. sibirica* var. *sibirica*, *C. sibirica* var. *bulbillifera*, and greenhouse grown specimens of *C. palustris*. Seasonal growth along shoots was identified by discrete regions of leaf scars that differ from each other in length and circumference along a continuous shoot axis.

RESULTS

Shoot Architecture

Claytonia sibirica var. *sibirica*. Perennials form an orthotropic to plagiotropic shoot with short internodes that bear helically arranged leaves, forming a rosette of photosynthetic leaves at the base of the newly elongating axis early in the growth season. Inflorescence branches and renewal shoots form in the axils of the basal leaves (Fig. 3A). The main axis of the shoot enlarges in length to approximately 1–2 cm over the growth season and becomes globose/ovoid (0.5–1.0 cm in diameter) at its distal end (Figs. 3A, 4A); however, shoot size is variable and appears to depend on the age and growth conditions of the individual. Shoots older than one season have a distal globose/ovoid region and a proximal cylindrical region that consists of stem produced in the preceding one or two growth seasons. The main axis of the shoot rarely consists of more than three growing seasons of growth. Some shoots retain their taproot up to their third growth season (Fig. 4B); however, more commonly the younger shoot axes disarticulate from older portions of rhizomes with taproots. The younger shoot axes form shoot-borne roots associated with nodes of the basal leaves.

When a new growth cycle commences, several whorls of foliage leaves expand before the first inflorescences emerge. Each inflorescence has a pair of opposite, sessile leaves (Fig. 4C) and each flower is subtended by a small, oblanceolate bract. Inflorescences develop initially from the axils of the distal leaves in the basal rosette. Subsequently, inflorescences can form in the axils of more proximal leaf positions in the basal rosette, although branches developing in these leaf axils can also form renewal shoots (Fig. 3A).

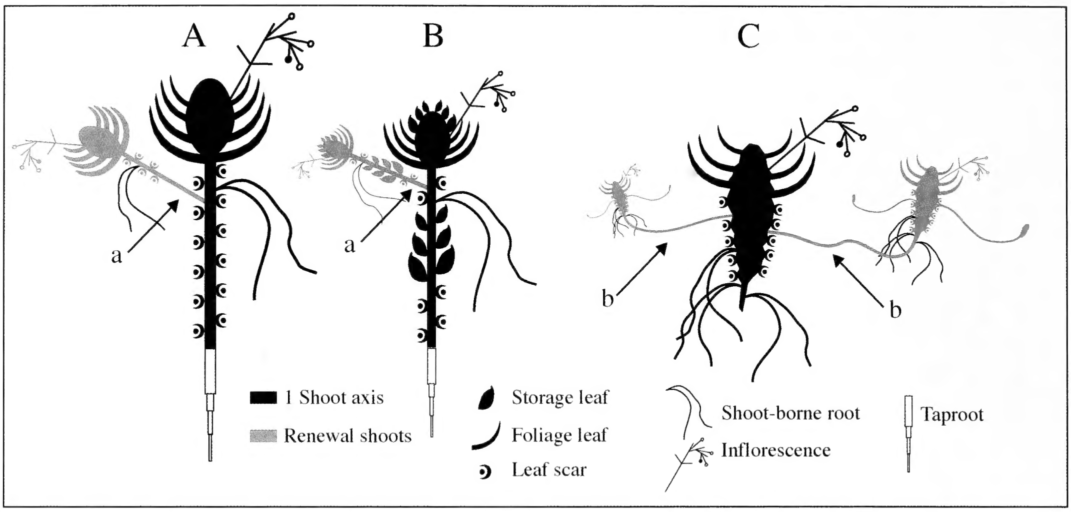

FIG. 3. Diagram of shoot system architecture in the *Claytonia sibirica* complex. A. *C. sibirica* var. *sibirica* B. *C. sibirica* var. *bulbillifera* C. *C. palustris*. Arrows labeled 'a' show aerial rhizomes, arrows labeled 'b' show hypopodia.

Renewal shoots have a basal rosette of helically arranged leaves. Elongation in the lower internodes of these axillary branches (below their rosette of foliage leaves) can create aerial rhizomes that extend renewal shoots 1–5 cm away from the main axis (Fig. 3A). Axillary, aerial rhizomes have shoot-borne roots associated with the nodes of the basal rosette leaves.

In most shoots, all leaves are foliage leaves and have a leaf base, petiole and lamina. Foliage leaves have a range of forms, varying in size depending on growing conditions and probably ploidy level, but range from 3–30 cm in overall length and 5-8 cm in blade width (Fig. 4C). Leaf bases are crescentic in cross-section and the width to thickness ratio increases as they age (Fig. 4D–F). Petioles are terete in cross-section and roughly twice the length of the lamina. The laminas of basal leaves in *C. sibirica* var. *sibirica* are generally deltoid (Fig. 4C); however, Miller et al. (1984) illustrate a wide range of variation in lamina shape in tetraploid and hexaploid populations. Foliage leaf color is consistently bright green for both eastern and western morphotypes.

Some ramets produce late season scale leaves in addition to foliage leaves. The scale leaves consist largely of leaf base and have a rudimentary petiole and lamina (Fig. 4G). This heteroblastic shift occurs uncommonly in populations of the western morphotype of *C. sibirica* var. *sibirica* but was not observed among any individuals from populations of the eastern morphotype.

Claytonia sibirica var. *bulbillifera.* This variety has shoot morphology distinct from that of *C. sibirica* var. *sibirica* in stature, habit, perennation strategy and leaf specialization. Its shallow, subterranean shoot system is consistently smaller than that of *C. sibirica* var. *sibirica*, and its growth habit more lax (Fig. 5A). *Claytonia sibirica* var. *bulbillifera* shoot systems are generally similar to those of var. *sibirica* in producing annually a globose/ovoid, orthotropic axis (Figs. 3B, 5B) that has a basal rosette of helically arranged leaves. Inflorescences form in the axils of leaves in the basal rosette as in *C. sibirica* var. *sibirica*. Renewal shoots that form in the axils of the earliest basal leaves can elongate as rhizomes.

Claytonia sibirica var. *bulbillifera* produces specialized storage leaves that have a swollen, succulent leaf base and an unexpanded petiole and lamina (Figs. 3B, 5C–G) at nodes distal to the foliage leaves in the latter part of the growing season (Fig. 3B). At the beginning of the next growing season, these storage leaves can be either decaying or still turgid (Fig. 5D). With the resumption of shoot growth, the axis thickens and elongates distal to the storage leaf zone, new foliage leaves expand as a basal rosette, and inflorescences elongate from those rosette leaf axils. Foliage leaves have a distinct leaf base, petiole and narrowly to broadly elliptic lamina (Fig. 5A), and they are often gray green with a reddish hue, especially when associated with sunny, serpentine sites. Shoot-borne roots emerge in the region between the storage leaves and the newly expanding foliage leaves. By late spring, storage leaves are produced distal to the foliage leaf zone (Fig. 3B). During the summer, shoot systems of *C. sibirica* var. *bulbillifera* produce a range of leaf types from the typical foliage leaf described above to a modified form of foliage leaf, which has a succulent leaf base and expanded petiole (Fig. 5F) and lamina, as well as storage leaves (Fig. 5C–G). Inflorescences continue to expand from axillary buds of all leaf

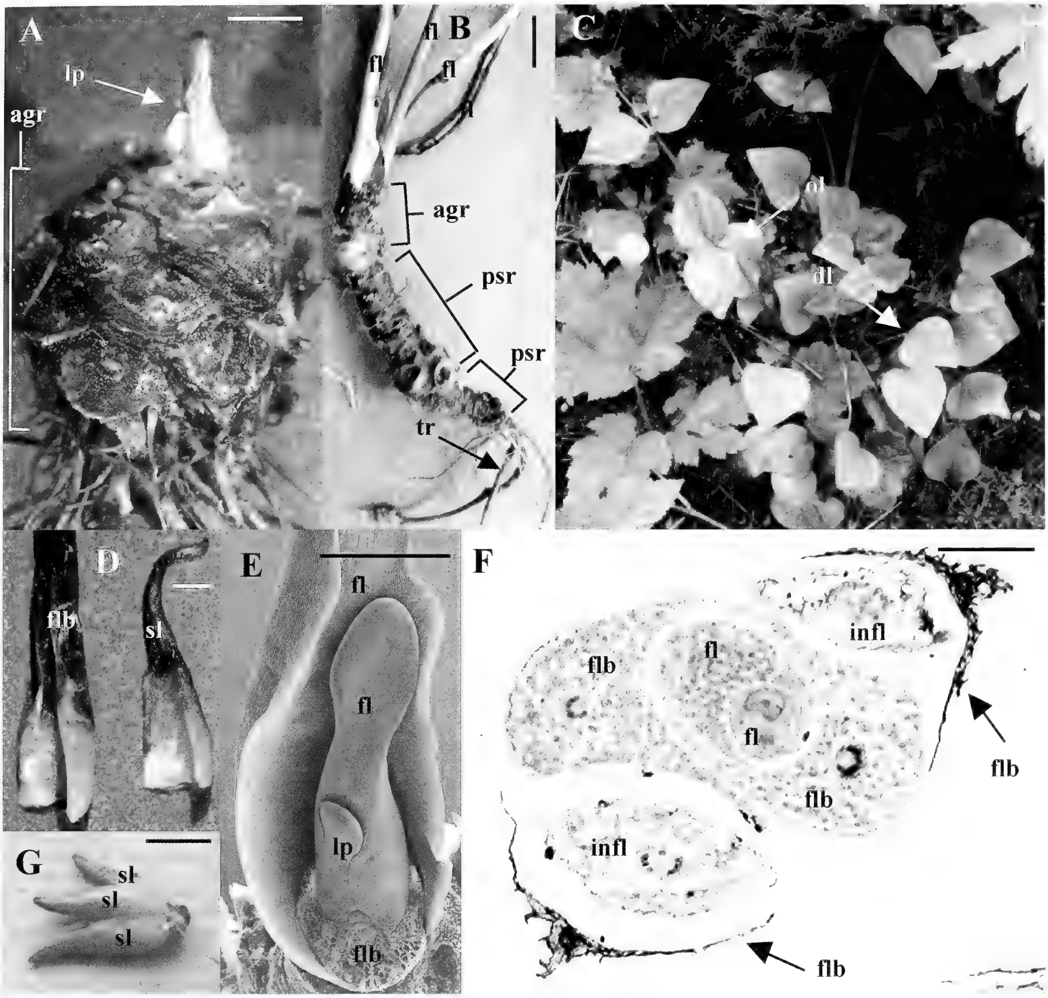

FIG. 4. Shoot system of *Claytonia sibirica* var. *sibirica*. A. Globose/ovoid shoot from active growth phase with foliage leaves and inflorescences removed (western morphotype). B. Shoot system of the eastern morphotype that shows three seasons of growth as discrete regions of leaf scars along a continuous shoot axis and retains a taproot. C. Habit. Arrows show opposite leaves subtending the inflorescence and deltoid lamina of the foliage leaf. D. Leaf base of foliage leaf (left) and scale leaf (right). E. Apex of a shoot system, showing the broad leaf base of a foliage leaf and two developing leaves. F. Cross section through the distal portion of a shoot showing the transectional shapes of leaf bases. G. Scale leaves that formed distally to the foliage leaves. agr = active growth rhizome, dl = deltoid lamina, fl = foliage leaf, flb = foliage leaf base, infl = inflorescence axis, lp = leaf primordium, ol = opposite leaves on inflorescence axis, psr = preceding season's rhizome, sl = scale leaf, slb = scale leaf base, tr = taproot. Scale bar = 3.0 mm in A; 2.0 mm in D, G; 1.86 mm in E; 1.0 mm in F; and 1 cm in B, C.

types throughout the growth season, which is extended for plants growing in more mesic sites. On drier sites, however, the above ground biomass withers and dies by late summer, leaving a shallowly subterranean shoot system that has prominent storage leaves (Fig. 5E). At the end of the growing season, *C. sibirica* var. *bulbillifera* preforms the foliage leaves and inflorescence buds that will expand during the next growing season.

Claytonia palustris. Claytonia palustris is shallowly subterranean and often submerged. It differs from the rest of the sibirica complex in habit, degree of internode elongation, vegetative reproduction, production of modified leaves and size. Shoot systems are weakly orthotropic to plagiotropic, consisting of a swollen ovoid stem with alternately arranged, sheathing leaves with dorsiventrally flattened bases. Leaves form in an open basal rosette that has longer internodes and fewer foliage leaves than the rosettes of the sibirica varieties (Figs. 3C, 6A–E). No leaf specializations for storage or perennation were observed in greenhouse grown or field-collected material. Greenhouse grown material grew only vegetatively. Renewal branches form in the axils of the lowermost leaves of the basal rosette and

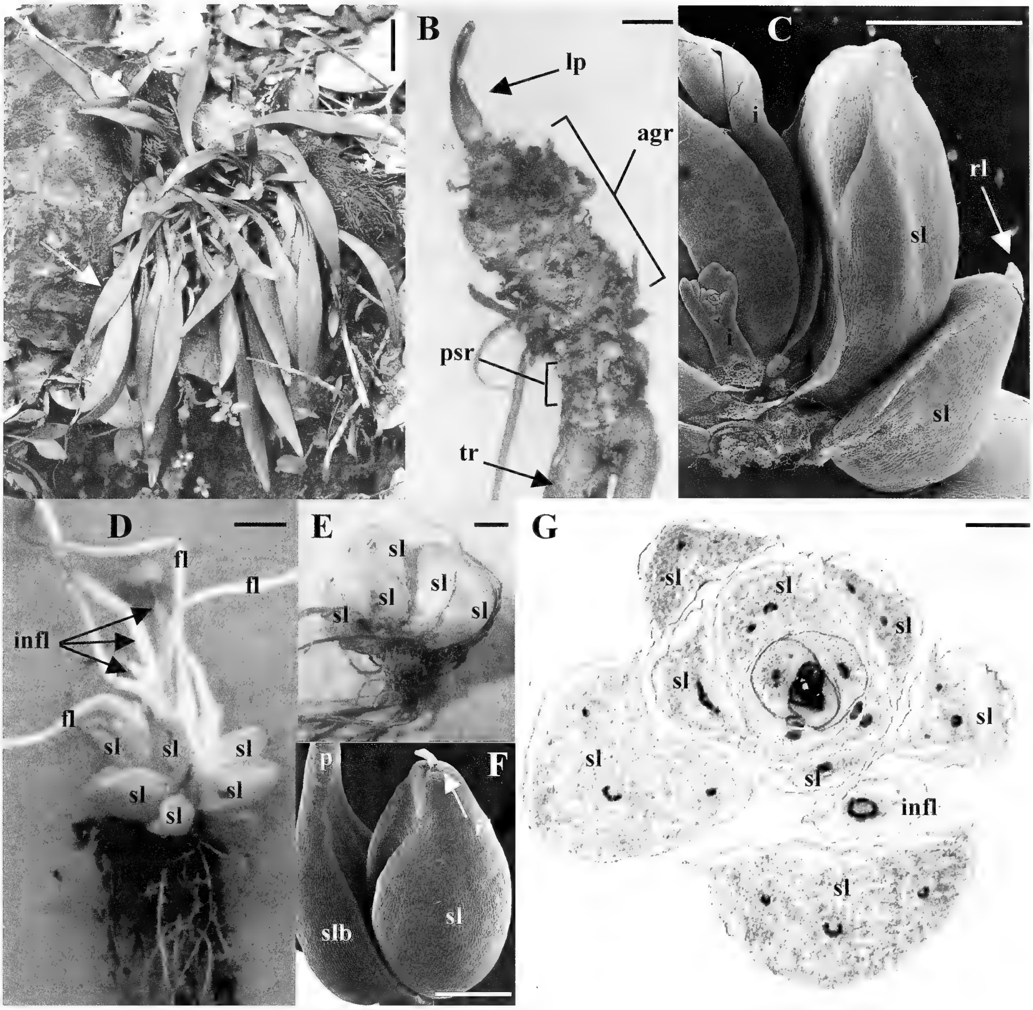

FIG. 5. Shoot system of *C. sibirica* var. *bulbillifera*. A. Habit. Arrow shows elliptical lamina of the foliage leaf. B. Dissected shoot system showing two seasons of growth. The stem is thicker in the region of active growth than for the preceding season. Foliage leaves, inflorescences and shoot-borne roots have been removed. C. Swollen scale leaves attached to distal portion of a rhizome. D. Shoot system showing overwintered scale leaves proximal to newly expanding foliage leaves and inflorescences. E. Subterranean bulb. F. Shoot system showing characteristics of transition from foliage to scale leaf zones. G. Cross section through distal portion of shoot showing transectional shape of scale leaves. agr = active growth rhizome, fl = foliage leaf, infl = inflorescence axis, lp = leaf primordium, p = petiole, psr = preceding season's rhizome, rl = rudimentary lamina, sl = storage leaf, slb = storage leaf base, tr = taproot. Scale bar = 1.0 cm in A; 2.0 mm in B, C, E; 5.0 mm in D; 1.0 mm in F, G.

inflorescences in the axils of the uppermost (Fig. 3C). Inflorescence axes have a subequal pair of oblanceolate to broadly elliptic leaves and flowers are subtended by small oblanceolate bracts. Under natural and greenhouse growth conditions, *C. palustris* has a size comparable to *C. sibirica* var. *bulbillifera*.

The axillary buds that become renewal shoots extend plagiotropically from the axils of rosette leaves and become highly elongated (5–15 cm) (Fig. 6D, E). Most of this elongation is in a single, basal internode (i.e., a hypopodium *sensu* Bell [1991]) that initially has a slightly swollen apical zone with unexpanded leaf primordia (Fig. 6E). The apical zone, (Fig. 6A) which consists of few nodes, becomes orthotropic, undergoes radial thickening in the axis, and foliage leaves expand. Shoot-borne roots are formed at nodes of these swollen, orthotropic renewal shoots, which then replicate the architecture of primary shoots over the course of the growing season.

Modified Leaves

A heteroblastic shift from foliage leaves to scale leaves was observed in all examined ramets of *C. sibirica* var. *bulbillifera* (Figs. 3B, 5D, 7), but was uncommon among ramets of *C. sibirica*

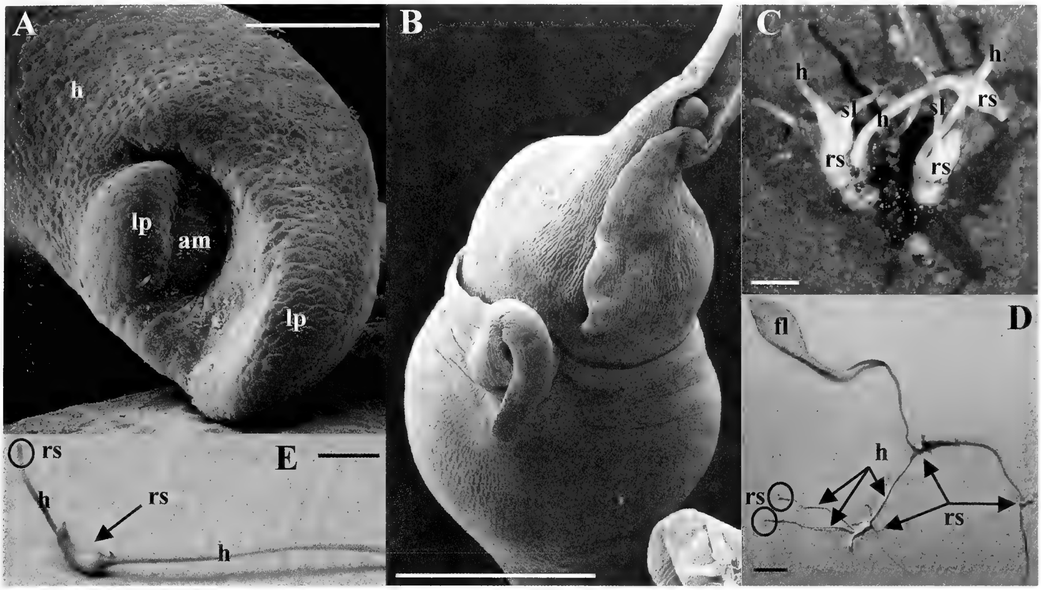

FIG. 6 Shoot system of *Claytonia palustris* A. Renewal shoot apex showing two leaf primordia at apical meristem. B. Renewal shoot showing prominently swollen axis apex. C. Renewal shoots. D. Stoloniferous habit. E. Renewal shoot with hypopodia. am = apical meristem, fl = foliage leaf, h = hypopodium, lp = leaf primordium, rs = renewal shoot, sl = scale leaf. Scale bars = 100 μm in A; 1.2 mm in B; 1.0 cm in D; 5 mm in C, E.

var. *sibirica*. The scale leaves of both varieties have rudimentary laminas that have a primordial shape and size and are frequently dislodged from the leaf base at maturity (Figs. 4D, G, 5C–F, 7A). All scale leaves are supplied by a single vascular strand, which broadens to form one medial and two lateral bundles that are embedded in a ground tissue of large, starch-filled, isodiametric cells. The epidermis is a single cell layer thick.

Scale leaf form, however, differs between the two varieties. Scale leaves of *C. sibirica* var. *sibirica* are similar in size and shape to the leaf bases of foliage leaves (Fig. 4D, F, G). In contrast, the scale leaves of *C. sibirica* var. *bulbillifera* are radially thicker than the bases of most foliage leaves, although transitional leaf forms that had a thickened base, short petiole, and small lamina were found among early season foliage leaves directly preceding the formation of foliage leaves (Figs. 5F, 7D). The thickening of scale leaves of *C. sibirica* var. *bulbillifera* is centered primarily in cells adaxial to the primary vascular strand, producing a flattened adaxial surface (Fig. 5C, G). In constrast, scale leaves of *C. sibirica* var. *sibirica* had limited adaxial thickening and retained the adaxial concavity of foliage leaf bases (Fig. 4D–F). Modified leaves in the western morph of *C. sibirica* var. *sibirica* were found only in late season collections and always in the distal portion of the shoot. This contrasts with our observations of *C. sibirica* var. *bulbillifera*, in which the late-forming scale leaves (i.e., storage leaves) persisted through the winter attached to the stem axis and were subjacent to the expanding foliage leaves and inflorescences of the next growing season (Fig 5D).

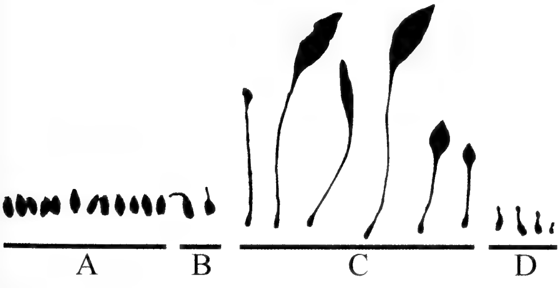

FIG. 7 Heteroblastic leaf series from one individual ramet of *Claytonia sibirica* var. *bulbillifera* (collected July 2004). A = Swollen scale leaves proximal to foliage leaves of the active growing season. B = Transition leaves with swollen bases, short petioles and small laminas. C = Foliage leaves. D = Swollen scale leaves at distal end of shoot.

DISCUSSION

Being a Bulb

Perennial members of the *C. sibirica* complex have similar globose to ovoid primary shoot axes that bear annually a basal rosette of leaves, from which axillary inflorescences and renewal shoots are formed (Fig. 3A–C). Although these shoot systems are fundamentally rhizomatous (*sensu* Bell 1991), some variants in the *C. sibirica* complex have been described as having bulbs,

bulblets, or bulbils, and being bulbiferous (Gray 1877, 1887; Miller et al. 1984). Thus, it is important to clarify the bulb aspects of shoot systems in the *C. sibirica* complex to understand how they represent modifications of the basic rhizomatous shoot system. Bulbs and bulblets are usually described as orthotropic shoot systems that bear fleshy (especially enlarged) scale leaves along very short internodes (Arber 1925; Rees 1972; Dahlgren and Clifford 1982; Bell 1991). Shoot systems of *C. sibirica* var. *bulbillifera* meet the criteria for bulb morphology. The production of relatively large, fleshy scale leaves between the cyclic intervals of reproductive growth seen in *C. sibirica* var. *bulbillifera* results in a bulb morphology that presumably serves as a perennation specialization of the basic rhizomatous form shared with other members of the complex. Gray's characterization of the KR form as having bulbs in a basal rosette (Gray 1877) and a crown of bulblet-scales (Gray 1887) calls attention to architectural variation: renewal shoots that formed in the axils of foliage leaves can have the form of bulbs when distal scale leaves swell late in the growing season and on the primary axis new succulent scale leaves of the current growing season would be formed as a crown distal to the foliage leaves. Bulbs of *C. sibirica* var. *bulbillifera* differ from those found commonly among various geophytic monocots. For example, geophytic monocots often have a thin, dry scale leaf or leaves (the tunic) that surrounds the entire bulb (Mann 1952; Rees 1972; McNeal and Ownbey 1973). Because they have very short internodes and leaves that lack petioles, it can appear that foliage leaves of geophytic monocots emerge from the rosette of fleshy scale leaves (Arber 1925; Dahlgren and Clifford 1982). Both of these distinctive aspects of monocotyledonous bulbs are lacking in *C. sibirica* var. *bulbillifera*, which has neither thin, dry scale leaves nor foliage leaves without petioles. Despite Dahlgren and Clifford's (1982) assertion that bulbs are a specialization found only in monocotyledons, we and others (Rees 1972; Cronquist 1981; Bell 1991), have recognized that a few clades of dicotyledons have also converged on bulb morphology.

Claytonia sibirica var. *bulbillifera* appears to be a serpentine endemic, and we hypothesize that the serpentine environment provided the selection for its bulb morphology. Kruckeberg (1984) discussed the general infertility of serpentine soils and the low turnover of nitrogen and phosphorus in communities associated with these soils. He emphasized that these unique nutritional and chemical characteristics have not only ecological but also evolutionary consequences, namely the origin of endemic species and subspecific ecotypes of plants adapted strictly to the serpentine environment. In the KR region, the growing season is limited largely to the late winter and spring and the above-ground foliage of herbaceous perennials has generally senesced by later summer. This relatively short growing season for herbaceous perennials in the KR is reminiscent of that faced by spring ephemerals of eastern deciduous forests. Lapointe (2001) emphasized that subterranean perennating structures, including bulbs, corms, thick rhizomes, and tubers, were evolutionary responses to the strong selection that spring ephemerals face for the rapid allocation of high levels of nutrients for shoot growth during the early spring when cool temperatures may limit enzymatic activity for photosynthesis. Herbaceous perennials of the KR region would face similar selection; moreover, this selection would be enhanced by the nutrient limitation of the serpentine environment. Thus, selection for a bulb morphology in this complex, in which ancestral heteroblastic variation would have included the formation of thick scale leaves as exemplified by *C. sibirica* var. *bulbillifera*, would help to circumvent the early season need for the rapid uptake of nutrients and augment the general nutrient-limited environment imposed by serpentine substrates by making nutrients available largely from scale leaves that are specialized for nutrient storage (and were provisioned over the course of the preceding growing season).

Morphological Transitions and Homology

Claytonia sibirica. Arber (1925) emphasized the morphological continuity between bulbs and rhizomes, and we observe this transition in *C. sibirica*. The shoot architecture of both varieties of *C. sibirica* is largely the same, but in var. *bulbillifera* we find specialization in the consistent formation of swollen scale leaves distal to the foliage leaves. At the end of the growing season, the bulb of var. *bulbillifera* consists of a tight aggregation of swollen storage leaves clustered around the preformed, but unexpanded, foliage leaves and inflorescences of the next growing season. Not all ramets of *C. sibirica* var. *sibirica* form scale leaves at the end of the growing season, but when scale leaves develop they have largely the size and shape of foliage leaf bases and are arranged in a relatively loose rosette at the tip of the shoot and are fewer in number than the swollen scale leaves of var. *bulbillifera* (cf. Fellows 1971). Given the positional and morphological similarity of scale leaves in both varieties, we hypothesize that they are homologous.

Miller et al. (1984) suggested that attributes of diploids, such as the morphotypes described here for varieties *sibirica* and *bulbillifera*, could have been combined in hybrid populations and this could account for the presence of scale leaves in some ramets of var. *sibirica*. Alternatively, the formation of scale leaves by some perennial

ramets of var. *sibirica* may simply represent variation in populations irrespective of hybridization or polyploidy. Instead these bulb-like modifications may be similar to the precursors of the distinctly bulbous var. *bulbillifera*. Additional populations of var. *sibirica* over its geographic range and habitat conditions need to be sampled for morphological variation, ploidy level, and ancestry to ascertain the phylogenetic homology of shoot system variants.

Claytonia palustris. In contrast to Miller's (1984) description of *C. palustris* as having "...branched rhizomes that are bulbiferous," we did not observe shoot systems in our sampling of this species that had the morphology of bulbs (cf. also Swanson and Kelley 1987). Primary and renewal axes of *C. palustris* become swollen and have short internodes that bear scale leaves at the end of the growth season, but these scale leaves do not enlarge as storage structures, a critical feature of bulbs. The initial elongation of axillary renewal shoots is centered in a single internode, a hypopodium (*sensu* Bell 1991), that functions in a manner similar to the droppers of various monocotyledonous geophytes, (e.g., *Erythronium*), in positioning the orthotropic portion of the renewal axis at a distance from the parent shoot (Arber 1925; McLean and Ivimey-Cook 1951). The hypopodia of *C. palustris* are homologous to the aerial rhizomes of other members of the *C. sibirica* complex but differ in the distance they remove renewal shoots from the parent plant. Aside from the formation of hypopodia during the initial elongation of renewal shoots, shoot architecture is very similar in *C. palustris* and *C. sibirica*. However, *C. palustris* is further distinguished from *C. sibirica* by the formation of leaf bases that completely ensheath the shoot axis, and these leaf bases lack the radial thickening that is common in *C. sibirica*.

Taxonomic Implications

Miller et al. (1984) did not recognize the morphotypes in the *C. sibirica* complex as different taxonomic entities, although they clearly describe morphological variation attributable to genetic differences. Chambers (personal communication) contends that *C. sibirica* exhibits a high degree of genetic variation over its wide latitudinal range but does not find clear delineations between types to warrant taxonomic recognition. However, plants cultivated from seed and grown over successive years under uniform greenhouse conditions show that plants from the KR maintain a strongly bulbiferous phenotype (O'Quinn unpublished data), from which we infer that shoot system plasticity in the formation of enlarged, fleshy scale leaves is limited. Because of their distinctive bulb morphology, discrete geographic distribution and preference for serpentine soils, we have followed Gray's (1887) treatment in recognizing KR populations as *C. sibirica* var. *bulbillifera*.

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SYSTEMATICS OF *SALVIA PACHYPHYLLA* (LAMIACEAE)

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ABSTRACT

Most populations of *Salvia pachyphylla* occur along mountain ranges adjacent to the Mojave Desert of southern California, southwestern Nevada, and northern Baja California, Mexico. A smaller disjunct group occurs in eastern Arizona near the southern edge of Navajo and Hopi reservation lands near Winslow, AZ. This study was undertaken to determine whether there are morphologically and genetically distinct geographical groups within *S. pachyphylla* and whether these groups form a cohesive unit easily separated from *S. dorrii.* Specimens of *S. pachyphylla* and broadly sympatric taxa in *S. dorrii* were examined in a morphometric analysis of twelve characters. A preliminary molecular analysis using the nuclear ribosomal DNA internal transcribed spacers (ITS-1 and ITS-2) and the embedded 5.8 S subunit was also performed on the same taxa. Morphometric analysis supports the continued recognition of *S. pachyphylla* and *S. dorrii* as distinct species and the recognition of three subspecies within *S. pachyphylla*, requiring two new subspecies, *eremopictus* and *meridionalis*, described here. The molecular data support the recognition of the *S. dorrii* species complex as a whole, but do not support the separation of *S. dorrii* and *S. pachyphylla* as distinct species, although the Mexican populations of *S. pachyphylla* appear genetically distinct.

Key Words: *Salvia pachyphylla*, disjunct distribution, morphometrics, sequence data.

Most *Salvia pachyphylla* Munz populations occur in the Transverse Ranges of the California Floristic Province and the mountain ranges of the Mojave Desert of southern California, southwestern Nevada, and northern Baja California Norte, Mexico. A smaller, disjunct group occurs in eastern Arizona near the southern edge of Navajo and Hopi reservation lands near the city of Winslow, AZ. This interesting disjunct distribution raises questions as to whether the geographical groups are morphologically distinct and whether these groups form a cohesive unit easily separated from *S. dorrii.*

Salvia pachyphylla was first collected by the Parish brothers in the San Bernardino Mountains and described as *Audibertia incana* var. *pachystachya* by Gray (1878). Samuel B. Parish (1898) elevated this taxon to *Audibertia pachystachya.* Amos A. Heller (1900) transferred *Audibertia pachystachya* to the genus *Ramona.* Harvey M. Hall (1902) transferred *Ramona pachystachya* to *Salvia* and recognized it as a variety of *S. carnosa* [now known as *S. dorrii*], giving it the name var. *compacta.* Philip A. Munz elevated it to species level (*Salvia compacta*), creating a homonym of *S. compacta* Kuntze (Munz 1927). Finally, Munz (1935) renamed *S. compacta* as *S. pachyphylla* Munz.

Salvia pachyphylla is a member of the *Salvia dorrii* (Kellogg) Abrams complex (Strachan 1982), which is comprised of only these two species. Epling (1938) and Strachan (1982) recognized the close relationship between *S. pachyphylla* and *S. dorrii* based upon morphological characters. They are both woody shrubs with peeling bark, opposite leaves in fascicles, and crowded verticils containing pink to magenta-colored bracts. Strachan (1982) used quantitative characters of the leaves and flowers to separate the two species. The leaves of *S. pachyphylla* are usually much larger than those of *S. dorrii* (20–50 mm vs. 4–30 mm). The inflorescence bracts the corollas are also much longer in *S. pachyphylla* (bracts 10–20 mm, corollas 17–28 mm vs. bracts 5–14 mm, corollas 9–18 mm in *S. dorrii*). One of the qualitative differences between the two species is the position of hairs on the corolla. *Salvia pachyphylla* has a ring of hairs within the lower portion of the corolla tube, whereas *S. dorrii* flowers possess hairs on the lower lip of the corolla that extend slightly into the throat. The distance between the base of the tube and the hairs is nearly the same in both species, which suggests that the length of the tube determines the final placement of the hairs (Strachan 1982). *Salvia pachyphylla* has hairs on the adaxial side of the bracts, whereas *S. dorrii* does not. The two species are hypothesized to be reproductively isolated because they are geographically isolated and flower at different times (Strachan 1982). *Salvia pachyphylla* flowers from July to October whereas *S. dorrii* flowers from March to July (September), which Strachan thought would exclude any gene flow. *Salvia pachyphylla* is found on north facing slopes at elevations of 1500–3050 m. The three subspecific taxa of *S. dorrii* found in the southwestern U.S.

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occur at much lower elevations (850–1900 m), even though Strachan (1982) noted higher elevations for the northern part of the range of var. *dorrii*.

Strachan (1982) noted that there may be three morphologically distinct groups within *S. pachyphylla*. The California plants have very large, obovate leaves (23–63 mm) and large bracts (11–20 mm). The Arizona plants have short, spatulate leaves (20–44 mm) and smaller bracts (8–14 mm). The Baja plants have small linear to narrowly spatulate leaves (26–45 mm) and intermediate bracts (10–19 mm). This morphological variation suggests either that the three groups have diverged or that the delimitation of *S. pachyphylla* from *S. dorrii* may have created artificial groups.

Two hypotheses are plausible: 1) *Salvia pachyphylla* once had a more continuous distribution across the Southwest until climate change, and subsequent contraction of pinyon-juniper woodland, split the species into the three groups seen today. If this was the case, one would expect to find some degree of morphological and genetic differentiation among populations across the range of the species; 2) The morphological variation seen in the Arizona populations of *S. pachyphylla* may be a reflection of a closer relationship between the Arizona populations and sympatric subspecies within *S. dorrii*. If this is true, one would expect to see more continuous morphological variation and genetic similiarity between the two species.

To resolve these issues the following questions were asked: 1) Are *Salvia pachyphylla* and *S. dorrii* distinct species? 2) Are there morphologically or genetically distinct geographical subgroups within *S. pachyphylla*? 3) If so, how much variation is found within the Arizona populations? 4) Can morphology or genetic markers be used to suggest an origin for the Arizona plants?

To answer these questions, morphometric analyses were performed on morphological characters and molecular sequence data were gathered from populations of *S. pachyphylla* throughout the geographical range of the species and populations representing the three subspecies of *S. dorrii* found in the Southwest. Morphometric analyses are commonly used to study variation among populations and species (Dodd and Helenurm 2000; Battaglia and Patterson 2001). Recent studies of the internal transcribed spacer region (ITS) (Baldwin et al. 1995; Ballard et al. 1999; Meerow et al. 2000; Urbatsch et al. 2000) have shown that this is a valuable region for phylogenetic studies at the species level and that the ITS region has enough nucleotide sequence variability for resolution of lower-level phylogenetic questions (Baldwin 1995; Soltis et al. 1998).

Methods

Morphometric Analysis

One hundred and eighty-two herbarium specimens were used in a morphometric analysis to determine morphological variation within the *Salvia dorrii* species complex. A complete list of the specimens used is included in Taylor (2002) and most are included in the exsiccatae listed in the taxonomic treatment below. Sample sizes are included in the figures below. Two specimens of *S. pachyphylla* from two different populations from Nevada were put into the California group due to similar morphological characters. Both *S. dorrii* subsp. *mearnsii* and *S. dorrii* subsp. *dorrii* were used in the morphometric analysis because populations of each exist in Arizona in close proximity to the populations of *S. pachyphylla*. Other varieties of *S. dorrii* were not used due to their physical distance from the Arizona populations of *S. pachyphylla*.

Calipers and a LEICA S6E (0.6–4×) dissecting scope were used to measure the 12 characters discussed below. Four categorical and eight continuous characters were used in the analysis. Measurement of bract length and width were determined by taking the average of three measurements using the lowest bract on the first full flowering verticil. Measurement of the hairs on the abaxial side of the bracts was made by averaging the majority of hair lengths. Hairs along the margin of the bract were calculated by averaging the five longest hairs along the margin. Corolla length was measured on rehydrated flowers at full anthesis. Rehydrated corollas were cut longitudinally to discern whether a ring of hairs was present within the corolla and whether there were hairs on the lip. Leaf length and width were averages based upon the three largest leaves on each specimen. The average of two internode lengths was taken starting at the base of the lowest bract and measuring to the base of the next to the last verticil. The adaxial side of the bracts was observed to determine the presence of hairs. The abaxial side of the bracts was observed to determine whether the glands were sunken into the leaf tissue or raised. Nine of the twelve characters (bract width, bract length, abaxial bract hair length, marginal bract hair length, corolla length, presence of hairs within corolla, leaf length, leaf width, internode length) were analyzed using the computer program SYSTAT version 8.0 (SPSS 1998) to perform a Discriminant Function Analysis (DFA) and Principle Components Analysis (PCA). Six of the 12 characters (bract length, bract width, leaf length, leaf width, internode length, corolla length) were analyzed through Analysis of Variance (ANOVA) using JMP version 4.0.4 (SAS Institute 2001).

TABLE 1. COLLECTION USED IN THE MOLECULAR ANALYSIS. All specimens deposited in the Deaver Herbarium (ASC).

Taxon	Locality	County/State	Collector/Coll. #	GenBank Accession #
Salvia pachyphylla AZ	Meteor Crater	Coconino Co., AZ	R. Taylor 03B	AF538906
	Meteor Crater	Coconino Co., AZ	R. Taylor 03C	AF538907
	N. Winslow	Navajo Co., AZ	R. Taylor 04C	AF538908
	N. Winslow	Navajo Co., AZ	R. Taylor 04E	AF538909
	Dilkon	Navajo Co., AZ	R. Taylor 26A	AF538911
	Dilkon	Navajo Co., AZ	R. Taylor 27	AF538912
	Petrified Forest	Coconino Co., AZ	R. Taylor 19	AF538910
Salvia pachyphylla CA	Santa Rosa	Riverside Co., CA	S. Rhodes 9924	AF538913
	Santa Rosa	Riverside Co., CA	S. Rhodes 9925	AF538914
	San Bernardino Mtns	San Bernardino Co., CA	S. Rhodes 9926	AF538915
	San Bernardino Mtns	San Bernardino Co., CA	S. Rhodes 9928	AF538916
Salvia pachyphylla MX	Sierra San Pedro Martir	Baja, Mexico	S. Rhodes 00124	AF538917
	Sierra San Pedro Martir	Baja, Mexico	S. Rhodes 00127	AF538918
Salvia dorrii subsp. Mearnsii	Cottonwood	Yavapai Co., AZ	R. Taylor 14A	AF538900
	Perkinsville	Yavapai Co., AZ	R. Taylor 15A	AF538901
	Sedona	Yavapai Co., AZ	R. Taylor 16D	AF538902
Salvia dorrii var. dorrii	N. Cameron	Coconino Co., AZ	R. Taylor 05C	AF543682
	Cameron	Coconino Co., AZ	R. Taylor 06A	AF538898
	Shadow Mtn	Coconino Co., AZ	R. Taylor 08	AF538899
Salvia dorrii var. pilosa	San Bernardino Mtns	San Bernardino Co., CA	S. Rhodes 9927	AF538903
	San Bernardino Mtns	San Bernardino Co., CA	S. Rhodes 9929	AF538904
	Kingston Mtns	San Bernardino Co., CA	S. Rhodes 9931	AF538905
Salvia mohovensis	San Bernardino Mtns	San Bernardino Co., CA	R. Taylor 13C	AF538921
	San Bernardino Mtns	San Bernardino Co., CA	R. Taylor 13E	AF53892
	San Bernardino Mtns	San Bernardino Co., CA	R. Taylor 11A	AF538920
Salvia davidsonii	Grand Canyon	Coconino Co., AZ	R. Scott 882	AF538919

Molecular Analysis

Twenty-six samples were used in the ITS analysis to represent the three geographic groups of *S. pachyphylla* and the three subspecific taxa of *S. dorrii* that are broadly sympatric (Table 1). *Salvia davidsonii* Greenm. and *S. mohavensis* Greene were used as outgroups for this analysis because they are southwestern representatives within the genus *Salvia* but have never been recognized as part of the *Salvia dorrii* species complex. *Salvia mohavensis* is placed within the same section *Audibertia* and sub-section *Jepsonia* as the ingroup (Epling 1938). Samples were taken from populations throughout the Southwest over a four-year period. The two Baja California, Mexico samples were obtained from herbarium sheets in the Deaver Herbarium (ASC).

Genomic DNA was extracted from silica-dried leaf tissue and fresh leaf tissue using a modified CTAB protocol of Doyle and Doyle (1987). Quality and quantity were assessed with gel electrophoresis on a 1% agarose gel. The entire ITS region (ITS 1/5.8 s/ITS 2) was then amplified using primers created with the Oligo program version 6.56; primer sequences are as follows: forward primer: ITSAL22F 5′ GTTTCCGTAGGT-GAACCTGC 3′; internal forward primer: IT-SAL291F 5′ CTCGGCAACGGATATCTCG 3′; and reverse primer ITSAL693R 5′ TTAAACT-CAGCGGGTGATCC 3′. DMSO was added to aid in the reduction of secondary structure (Soltis et al. 1998). Amplification procedures were as follows: four minutes of denaturing at 95°, thirty seconds at 95°, thirty seconds of annealing at 55°, one minute of extension at 72°, thirty two cycles, ten minute extension at 72°, and a holding temperature at 4°.

To assess possible parology, Polymerase Chain Reaction (PCR) products were cloned, due to noise within the sequence and problems with amplification. Cloning was accomplished using an Invitrogen TOPO TA cloning kit (Electroporation protocol) following the manufacturer's recommended procedures. Amplification of the clones were as follows: Five minutes of denaturing at 95°, thirty seconds at 95°, thirty seconds of annealing at 56°, one minute of

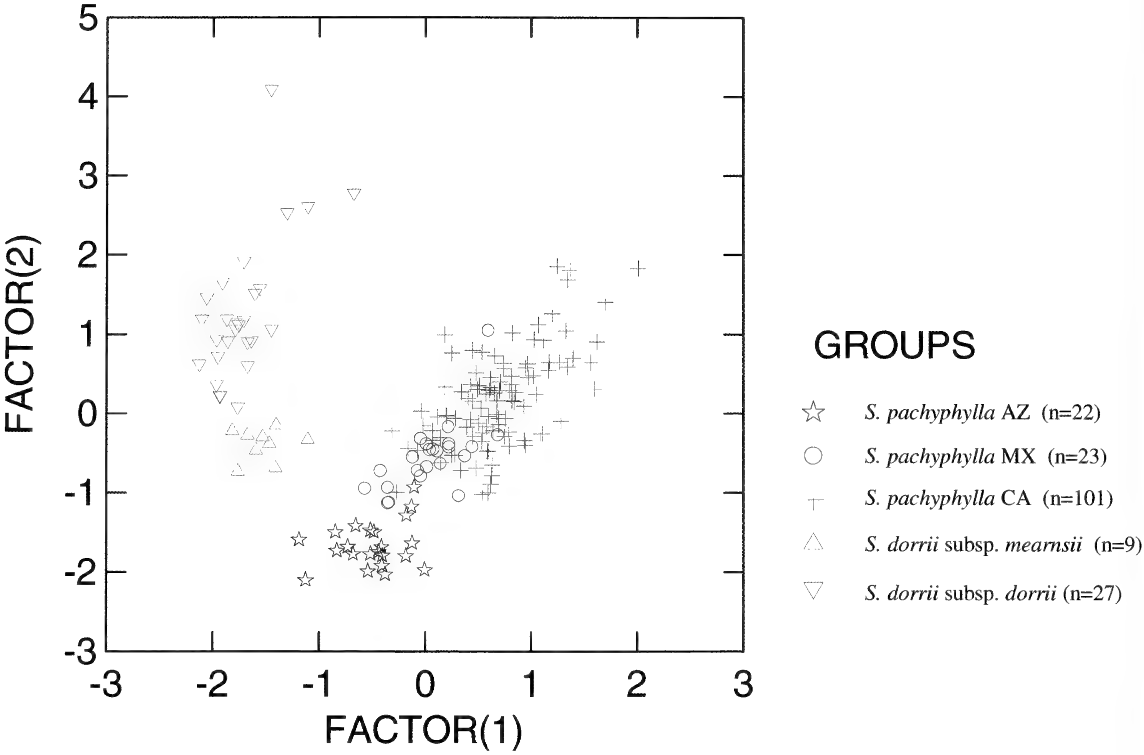

FIG. 1. PCA scatter plot of morphological characters. Factor 1 is the first principal component and Factor 2 is the second principle component. Sample numbers (n) for each taxon in parentheses. See text for discussion of factors.

extension at 72°, thirty five cycles, three minute extension at 72°, and a holding temperature at 4°. PCR concentrations and amplification were assessed electrophoretically on a 1% agarose gel using a low DNA mass ladder. No length mutations were seen in any of the clones. PCR products from three clones were purified using Qiagen's QIAquick PCR purification columns and protocols. Double-stranded PCR products were sequenced on polyacrylamide gels at the Arizona Research Lab in Tucson using a big dye terminator chemistry kit version 2 and an ABI 377 machine.

Forward and reverse sequences and ABI electropherograms were edited in DNA STAR-Seqman II version 5.01 (1989;–2001) after reverse complementation to resolve any ambiguities. Sequences were placed in DNA STAR-Megalign version 5.01 (1993;–2001) and aligned using Clustal W and then aligned visually. All but one of each set of redundant sequences were excluded from the alignments. Sequence alignments were saved as PAUP files and analyzed using PAUP 4.0b10 (Swofford 2002). Heuristic searches were performed with tree bisection and reconnection (TBR) branch swapping and random taxon addition. All searches were run using only informative characters. Gaps were coded as missing data and as a 5th element. One hundred bootstrap replicates were performed using the heuristic search and TBR branch swapping.

RESULTS

Morphometric Analysis

Principal component analysis (PCA) of all specimens produced the scatter plot shown in Fig. 1. The factors (i.e., principal components) are linear combinations of characters that best account for variation in the data. The first factor was comprised mostly of bract length, corolla length, ring of hairs, leaf length, and leaf width. Factor two was comprised mainly of one character, bract hair length. The loadings of variables for each factor can be found in Taylor (2002).

The principle components analysis shows clear separation between *S. dorrii* and *S. pachyphylla*. Clear separation is also seen between the Arizona populations and the California populations of *S. pachyphylla* although the Mexico specimens overlap with both the Arizona and California clusters. The PCA results were identical when examining scatter plots containing specimens of *S. pachyphylla* and *S. dorrii* together or just examining scatterplots containing only *S. pachyphylla* specimens (PCA not shown), the trends still remain

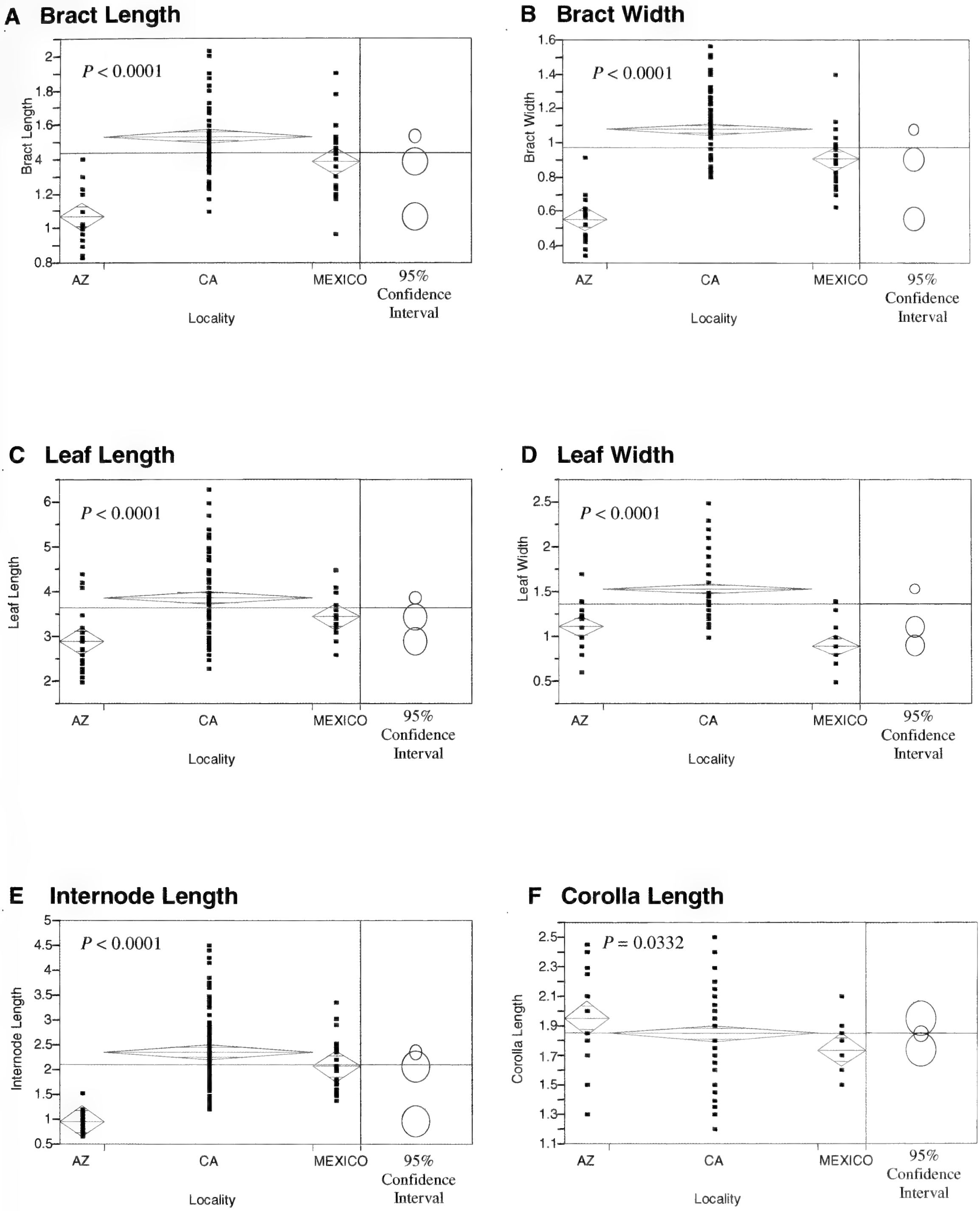

FIG. 2. Distribution and 95% confidence intervals for six morphological characters in *S. pachyphylla* separated by locality. Horizontal line represents overall mean for all groups. Diamonds show means (center line) and the 95% confidence limits (top and bottom lines) for each group. Circles also represent the 95% confidence intervals for each group.

the same between the *S. pachyphylla* geographic groups (Taylor 2002).

The distributions and 95% confidence intervals for six of the nine morphological characters are shown in Figure 2. All six characters showed significant differences among the three geographical groups of *S. pachyphylla* (ANOVA, $P < 0.05$). For five of the six morphological char-

TABLE 2. CLASSIFICATION MATRIX OF ALL SPECIMENS USED IN THE MORPHOMETRIC ANALYSIS.

		A	B	C	D	E	% CORRECT
A	*S. pachyphylla* AZ	21	0	1	0	0	95
B	*S. pachyphylla* MX	1	21	1	0	0	91
C	*S. pachyphylla* CA	1	12	88	0	0	87
D	*S. dorrii* ssp. *mearnsii*	0	0	0	9	0	100
E	*S. dorrii* ssp. *dorrii*	0	0	0	0	27	100
TOTAL		23	33	90	9	27	91

acters, P values were less than 0.0001. All pairs of the three geographical groups had significantly different means ($P < 0.05$, Each Pair Student's t-test). The Mexican populations appear intermediate between the California and Arizona populations with respect to bract shape (length and width), and internode length. The California populations appear intermediate in corolla length, while the Arizona populations appear intermediate for leaf width and hair length on the floral bracts.

The classification matrix, derived from a Discriminant Function Analysis (DFA) was used to test group membership based on pre-defined geographic distributions of *S. pachyphylla*. The classification matrix presented in Table 2 had percentages of correct grouping ranging from 87–100%. This matrix indicates complete taxonomic separation between populations of *S. pachyphylla* and *S. dorrii*. No misidentifications were seen. The matrix also provides adequate support for the recognition of all three geographical groups as subspecific taxa within *S. pachyphylla*. Based upon the matrix produced, the Arizona and Mexican specimens will rarely be misidentified (91–95% correct placement), while the morphological variation found in the Californian populations may result in correct placement only 87% of the time. Only a few of the Californian specimens showed extreme variability. Most of the Californian specimens contributed to the limited variability seen in the results discussed above. A jackknife matrix derived from an analysis of all specimens using the same groupings ranged from 85–100% correct grouping (Taylor 2002).

Molecular Analysis

Sequence characteristics of the ITS region within the *S. dorrii* complex and outgroups are summarized in Table 3. Sequences from cloned DNA showed no variation that would suggest that paralogues were present. Sequences obtained for the ITS 1 region are within the ranges reported by Baldwin et al. (1995), but the size in base pairs (268–277) is larger than all taxa reported, except for the Brassicaceae and Malvaceae. The ITS 2 region is within the reported base pair range. The ITS 1 region also contains 2–7% higher sequence divergence compared to the ITS 2 region. Levels of divergence within the *S. dorrii* species complex, including both ITS regions and the 5.8 S, ranged between 0.1–7.7%. The levels of divergence were much higher when the outgroups were included with ranges between 9.3–28.8%. Rates of divergence are consistent with other studies that compare lower level taxa (Schilling et al. 1998). The G+C content within the ITS 1 and ITS 2 are similar to each other and are much higher than G+C content found in all other families except Rosaceae (Baldwin et al. 1995).

Of the 695 nucleotide positions sequenced during this molecular analysis, 71 were parsimony informative. One hundred equally most parsimonious trees (length 85) were found using 10 random sequence additions with all characters equally weighted and gaps coded as missing data (consistency index (CI) = 0.90, retention index (RI) = 0.94, rescaled consistency (RC) = 0.84) (Fig. 3). One hundred equally parsimonious trees (length 95) were also found using gaps coded as

TABLE 3. SEQUENCE CHARACTERISTICS FOR THE *SALVIA DORRII* COMPLEX AND OUTGROUPS.

	ITS 1	ITS 2	5.8 S
Aligned Length	268	252	162
Un-aligned Length	268–277	243–252	162
Sequence Divergence within *S. dorrii* complex (%)	0.1–7.7	0.1–2.5	0.1–1.2
Sequence Divergence including outgroups (%)	13.1–28.8	11.0–21.4	9.3–10.6
G+C Content (%)	65–71	61–71	49–58
Informative Sites within *S. dorrii* complex	5	6	1
Informative Sites including Outgroups	26	29	16
Informative Sites within *S. dorrii* complex gaps as 5th state	5	8	n/a
Informative Sites including Outgroups gaps as 5th state	93	34	n/a

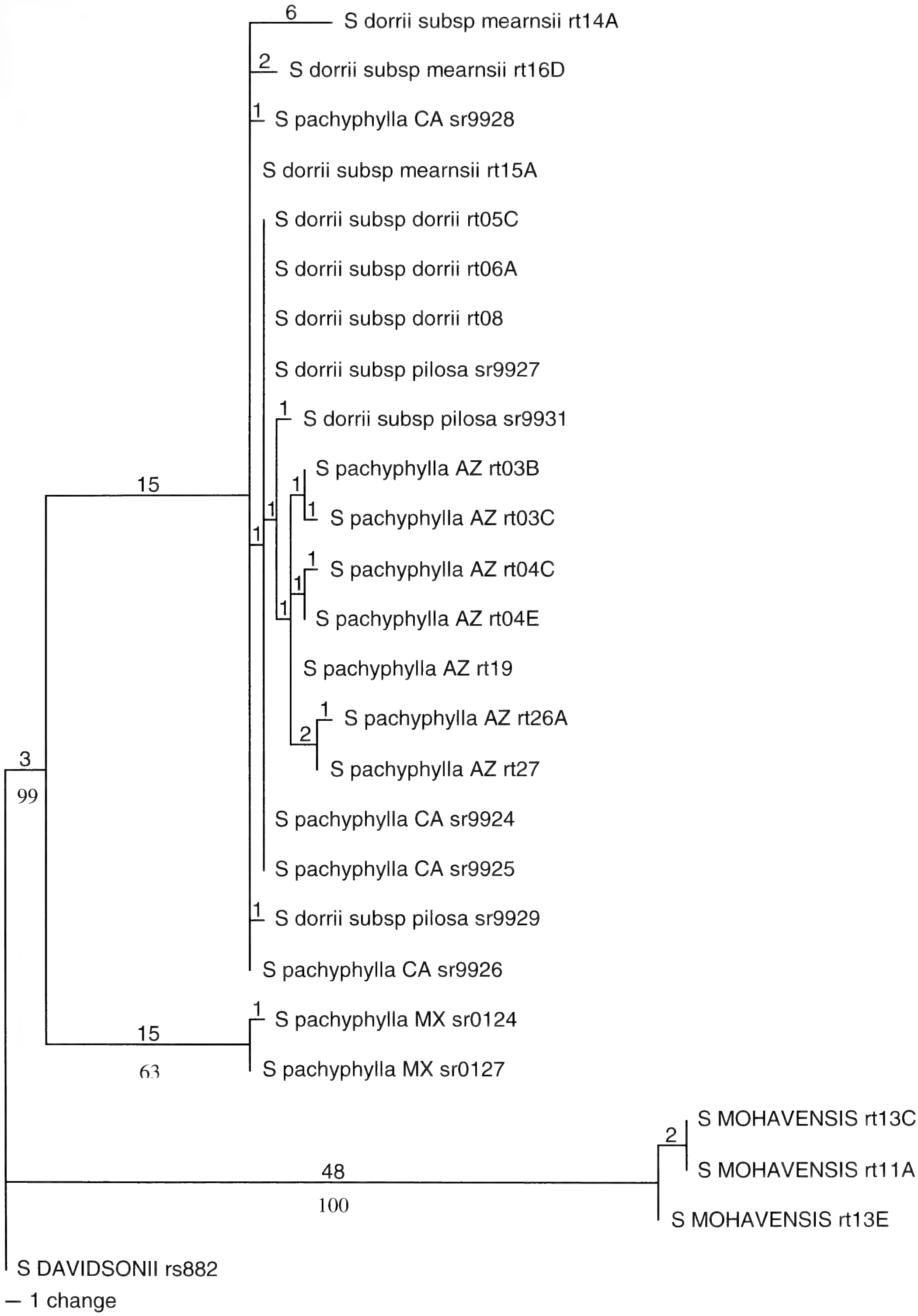

FIG. 3. Phylogram of ITS sequence data; one of one hundred equally most parsimonious trees showing branch lengths above the nodes and bootstrap support for selected nodes; initials after taxon names refer to collector/collection numbers: rt = R. Taylor collections; sr = S. Rhodes collections; rs = R. Scott collections.

a 5th state (CI = 0.90; RI = 0.94). No major changes in topology were evident by coding gaps as missing or as a 5th state. There is little resolution between *S. pachyphylla* and the taxa sampled from the *S. dorrii* complex with one notable exception, the *S. pachyphylla* specimens from Mexico. The *S. pachyphylla* populations from Mexico appear genetically distinct from all of the rest of the *S. dorrii* complex. The *S. pachyphylla* populations from the Arizona group form a weak clade. There is no support for a group representing the *S. pachyphylla* populations that occur in California. The *S. dorrii* complex as a whole formed a strong clade (bootstrap = 99%).

Discussion

The morphometric data not only suggest continued recognition of *S. dorrii* and *S. pachyphylla* as separate species, but the data also support recognition of three distinct groups within *S. pachyphylla*. The molecular data do not fully reflect the amount of morphological divergence seen in the *S. dorrii* species complex. The molecular data show strong support for the *S. dorrii* complex as a whole but provide little else, except that the Mexican populations of *S. pachyphylla* appear to be genetically distinct from the rest of the *S. dorrii* complex. Lack of molecular divergence has been documented in the Asteraceae where morphology evolves faster than DNA sequences even in rapidly evolving gene regions (Baldwin et al. 1998; Baldwin 2000). ITS sequences in woody plants evolve much more slowly than ITS sequences in herbaceous annuals of recent origin (Baldwin et al. 1995). Some populations of *S. pachyphylla* and *S. dorrii* subsp. *mearnsii* have large, gnarled trunks with peeling bark, which suggests that they may be very long-lived shrubs. A small pilot study looking at the 3′ end of *mat*K and its adjacent spacer region of the chloroplast DNA of four taxa within the *S. dorrii* complex corroborates the ITS results and suggests that *S. pachyphylla* may be paraphyletic (Taylor 2002).

Many different Native American tribes have used both species within the *Salvia dorrii* complex for medicinal or ceremonial purposes in the past and some continue to use it today (Zigmond 1981; Huisinga 2001). *Salvia pachyphylla* currently is wild-harvested by the Navajo and Hopi as ceremonial tobacco and medicine (Phyllis Hogan personal communication). Trade can function as a mode of transportation to a new locality, which can help organisms overcome geographical barriers enabling genetic and morphological differentiation (Brooks and Johannes 1990). Most populations of *S. pachyphylla* occurring within Arizona are found in close proximity to ruins, suggesting that they might be products of prehistoric introduction. If the Arizona populations had shown little or no morphological or genetic variation and had nested within one of the other geographical groups, this mode of introduction, although untestable, might have been more plausible.

The results of the PCA and ANOVAs show that there has been significant morphological differentiation of all *S. pachyphylla* populations in Arizona when compared to the California and Mexico populations. These results thus refute the possibility that the Arizona populations were remnants of trade between groups of indigenous peoples. In addition, there is evidence that the presence of the species predated human migration into northern Arizona. Plant macrofossils from packrat middens are an ideal method for reconstructing past plant species distributions and ages (Cole 1990). The Cricetid rodent, *Neotoma stephensi* (the packrat), has been known to collect plant material within a 30–100 meter radius from the nest for nest building materials (Van Devender et al. 1987). Packrat urine contains high amounts of calcium oxalate, which aids in solidifying the midden into rock-like deposits (Wells 1976). The crystallized urine envelops and protects the plant macrofossil from decay, preserving it for years to come (Cole 1990). It has been shown that midden deposits are preserved for over 50,000 years in optimal conditions (Wells 1976; Cole 1990).

Material from packrat middens show species within the *S. dorrii* complex to be at least 39,900 years old based on carbon dating of leaves (K. Cole unpublished data). Leaves of *S. pachyphylla* found in Nevada have been dated to between 10,060–11,940 years old (K. Cole unpublished data), which predates Archaic Cultural Groups of PaleoIndians (Fish and Fish 1984). Samples of *S. dorrii* subsp. *dorrii* from packrat middens found in Arizona have been dated between 12,015–17,400 years old (K. Cole unpublished data). There are no known specimens of *S. pachyphylla* from middens in Arizona to date, but, based upon the midden data presented above, it is plausible that *S. pachyphylla* occurred in Arizona well before settlement by PaleoIndian groups. The present day distribution of the three extremely small populations of *S. pachyphylla* in Arizona adjacent to ruins may be the result of past wild-harvesting or natural remnant populations that are soon to become extinct. The fourth Arizona population of *S. pachyphylla* is extensive and has very large individuals, seedlings, and many different intermediate age classes indicating that the occurrence of *S. pachyphylla* in Arizona is probably not a remnant of past use by Paleoindians.

The research presented here is not definitive but suggests that the distribution of *S. pachyphylla* was once more continuous, with vicariant

events causing the contraction of the populations to the geographically distinct groups seen today. This vicariance might have been caused by climate changes such as rising temperatures and decreasing moisture during the formation of the Mojave Desert (Raven and Axelrod 1978; Stott 1981; Axelrod 1983; Schaffer 1993). The contraction to the current disjunct distribution in Arizona might also have occurred as late as the Holocene, when pinyon-juniper woodland again dominated the landscape until warmer, drier climate resembling present day conditions occurred at the end of the Pleistocene (Martin and Mehringer 1965). Examples of disjuct distributions from northern Baja California, Mexico and northeastern Arizona are known from other taxa such as *Errazurizia* Phil. and phylogenetic studies of these groups might lead to a better understanding of southwestern biogeography.

Results of the morphological data support the recognition of subspecific taxa within *S. pachyphylla*, as presented below. Due to the size of most of the Arizona populations and the importance of this plant to tribes in the Southwest, monitoring of populations and of annual harvesting is recommended. Future research within the *S. dorrii* complex should include larger sample sizes, additional molecular markers, and ecological observations to understand whether the recognition of one or two distinct species within the *Salvia dorrii* species complex is warranted.

Taxonomic Treatment

Salvia pachyphylla Munz Rose Sage

Aromatic, branching perennial shrub with gray peeling bark 35–100 cm tall 40–150 cm wide, generally much wider than tall. LEAVES opposite, fascicled, glandular, 2.0–6.3 cm long and 0.5–2.5 cm in wide, fleshy, obovate to rhombic, attenuate at the base of the leaf, tip acute to obtuse, abaxial and adaxial sides covered in appressed white hairs. INFLORESCENCE of 1-many verticils subtended by many bracts; bracts green to magenta in color, glandular, ciliate, scarious, rotund to orbicular, pubescent. FLOWERS several per verticil; calyx connate, lobed at the top, green to purple, pubescent; corolla connate, blue to violet, limb comprised of an upper lip and two bilateral lobes, tube containing a ring of hairs; stamens 4, exerted from corolla. FRUIT 1–4 nutlets. SEEDS tan to black. Found on north facing slopes in conifer forests, 1219–2830 m (4000–9284 ft). Three subspecies distributed in southwestern North America (Fig. 4). Uses: smoke or tea to calm the mind, and used in the treatment of epilepsy (Whiting 1939; Zigmond 1981).

Key to the Subspecies of *S. pachyphylla*

1. Internode length between verticils (6.5-) 8.5–10 (-15.5) mm, bract width (3.5-) 5.5–5.9 (9.2) mm, endemic to northeastern Arizona . . . . *S. pachyphylla* subsp. *eremopictus*
1. Internode length between verticils (14.5-) 18.5–25 (-45) mm, bract width (6.5-) 9–13 (-15.7) mm.
2. Shrubs with a well-defined woody trunk, leaf length (2.6-) 3–3.6 (-4.4) mm, leaf width (5-) 7–11 (-14) mm, endemic to Baja California, Mexico . . . .*S. pachyphylla* subsp. *meridionalis*
2. Subshrubs mostly branching below the ground, leaf length (2.3-) 3.7–4.2 (-6.3) mm, leaf width (10-) 13–17 (-25) mm, southern California and Nevada . . . . *S. pachyphylla* subsp. *pachyphylla*

Salvia pachyphylla P. A. Munz subsp. *pachyphylla* Rose Sage Illustration: Brittonia 34(2): 167. 1982.

Audibertia incana var. *pachystachya* A. Gray, Syn. Fl. N. Amer., ed. 2. 2(1): 461. 1886. *A. pachystachya* Parish, Erythea 6:91. 1898; not *Salvia pachystachya* Trautv. *Ramona pachystachya* A. A. Heller, Muhlenbergia 1:4. 1900. *Salvia carnosa* var. *compacta* H. M. Hall, Univ. Calif. Publ. Bot. 1:111. 1902, nom. superfl. *S. compacta* Munz, Bull. S. Calif. Acad. Sci. 26:22. 1927; not *S. compacta* Kuntze, 1891. *S. pachyphyulla* Epling ex Munz, Man. S. Calif. Bot. 445. 1935. Type: UNITED STATES. California: San Bernardino Co.: Bear Valley, San Bernardino Mts., Aug 1882, *Parish & Parish 330* (lectotype, GH; isolectotypes A, DS, F).

Subshrubs extensively branching below the ground, 30–45.5 cm tall, 61–120 cm wide. INTERNODES 1.2–4.5 cm. LEAVES obovate, 2.3–6.3 cm long, 1.0–2.5 cm wide. FLOWERS 1.2–2.5 cm long. BRACTS many; 1.1–2.03 cm long; 0.8–1.57 cm wide; hairs on bracts 0.01–0.02 mm long; hairs on bract margins 0.01–0.055 mm. SEEDS 3 mm long, 2 mm wide.

Paratypes. U.S.A., California. Inyo Co., Panamint Mtns, Death Valley National Monuemnt, Aguereberry Point, 1961 m, 02 July 1983, *R.F. Thorne 56130.1* (RSA); Jail Canyon, 2438 m, 11 July 1977, *A.P. Romspert 13* (RSA); Rogers Peak, 2591 m, 10 July 1974, *L. DeBuhr 44818* (RSA); Wildrose Canyon, 1920 m, 3 July 1974, *L. DeBuhr 44793* (RSA); T19S R45E sect. 27, 1951 m, 15 August 1968, *J.L. Reveal 1786* (RSA); Dolomitic Rocky Ridge, UTM 497130E, 4023510N, 1951 m, 2 July 1983, *P.M. Peterson 1183* (RSA); Narrow Canyon above Townes Pass, 17 June 1937, *C. Epling* (RSA); Thorndike's Ranch, 2286 m, 7 July 1937, *C. Epling* (RSA);Wild Rose Canyon to Telescope Peak, 2682 m, 8 July 1937, *P.A. Munz 14793* (RSA); 2133 m, 16 May 1931, *R. Hoffmann 459* (RSA); Kern Co., Scodie Mtns, Walker Pass Trailhead on Pacific Crest Trail, T26S R37E sect. 19, 1707 m, 6 August 1988, *B.*

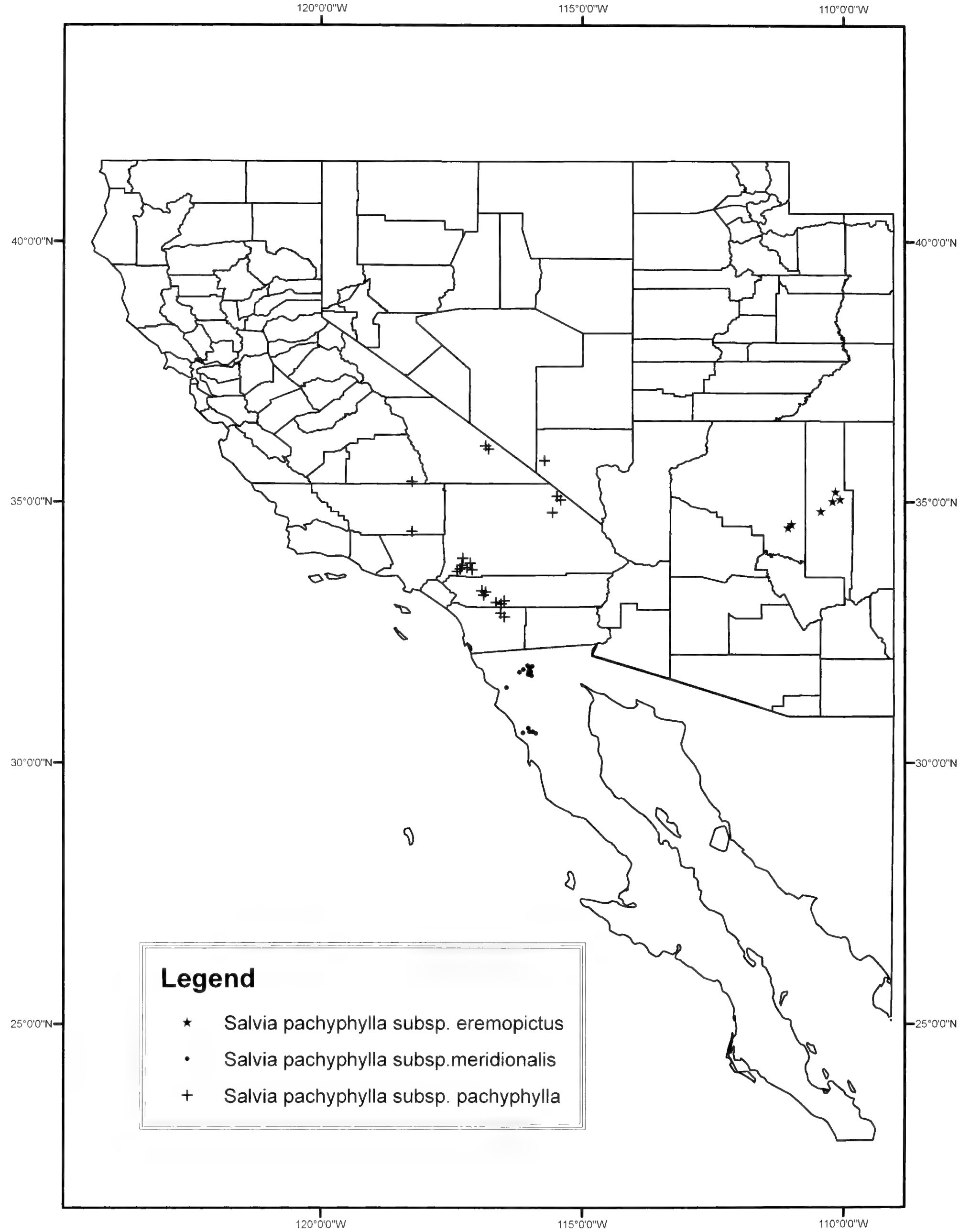

FIG. 4. Distribution of the three subspecies of *Salvia pachyphylla*.

Ertter 7891 (NY, RSA); Riverside Co., San Jacinto Mtns, 1402 m, June 1901, *H.M. Hall 2160* (NY, RSA); north slope, 1829 m, 20 August 1922, *E.C. Jaeger 1010* (RSA); Tahquitz Peak, 22 August 1933, *L. Crutcher 3* (RSA); Tahquitz Valley, 2652 m, 31 August 1930, *J. Ewan 2149* (RSA); Santa Rosa Mtns, 1981 m, 21 August 1952, *P.A. Munz 17995* (NY, RSA); 2 September 1970, *C.W. Tilforth 297* (RSA); dry slopes, 2134 m, 29 June 1922, *P.A. Munz 5888* (RSA); near Santa Rosa Springs campground, 2088 m, 15 June 1978, *C. Davidson 7382* (RSA); 2138 m, 21 August 1971, *N.R. Zabriskie 438* (RSA); near Vendeventer Flat, 1676 m, 1 July 1933, *V. Duran 3490* (NY,RSA); stony slopes near creek, 1524 m, 25 June 1922, *P.A. Munz 5813* (RSA); Toro Peak, 2438 m, 14 August 1938, *P.A. Munz 15363* (RSA); Vandeventer Flat, 2073 m, 21 August 1952, *P.A. Munz 17981* (NY, RSA); Cultivated, 2 September 1954, *E.K. Balls 19778* (NY, RSA); virgin spring, 2652 m, 14 August 1938, *P.A. Munz 15346* (RSA); Toro Mtn, July 1901, *E.E. Schel-*

lenger (RSA); San Bernardino Co., Blk. Hawk Mine, near Victorville, 4 July 1926, *M.E. Jones* (RSA); Clark Mtns 4.2 miles NNW of Mountain Pass, 2134 m, 6 July 1972, *B. Prigge 2* (RSA); 4 miles NW of mountain pass, 2250 m, 6 July 1973, *B. Prigge 1197* (NY, RSA); Pachalka Spring, 1981 m, 6 October 1935, *C.B. Wolf* (RSA); Hanna Flats, near Fawnskin, 1829 m, 23 July 1941, *G.T. Hastings* (NY); Keystone Mine, 45(air)miles E of Baker, 5.5 (air)miles S of Ivanpah at Jct. Roads to Keystone Mine and Keyston Springs, 1680 m, 29 August 1973, *J. Henrickson 12620* (RSA); Kingston Mtns, 2 miles from peak, 1676 m, 23 October 1977, *J. Henrickson 16297* (RSA); Kingston VABM, 2136 m, 18 September 1980, *S. Castagnoli 228* (RSA); Mid-Shut-Up canyon, 1524–1676 m, 23 October 1977, *J. Henrickson 16305* (NY); on a rocky ridge, 2134 m, 27 July 1949, *J. Roos 4507* (RSA); Porcupine Canyon, 2134 m, 21 September 1980, *R.F. Thorne 54790* (RSA); New York Mtns, Keystone Canyon, 1580 m, 7 July 1973, *J. Henrickson 11056* (RSA); 1737 m, 29 October 1976, *R.F. Thorne 47965* (RSA); 29 July 1952, P.C. Everett 17299 (RSA); Keystone Spring, 1707 m, 13 October 1935, *P.A. Munz 13874* (RSA); San Bernardino Mtns, 8.7 miles SE of Lucerne Valley, 1398 m, 18 June 1978, *C. Davidson 7300* (RSA); Barton Flats, 1981 m, 30 October 1955, *L. Benson 15607* (RSA); Bear Lake, 2000 m, 7 July 1931, *E.W. Clokey 5292* (NY); Bear Valley, 1 August 1901, *L.R. Abrams 2077* (RSA); 1895, *A. Davidson* (RSA); Big Bear Lake, 22 August 1935, *C.L. Hitchock 2825* (RSA); 6 July 1924, *J.M.J.* (RSA); 8 August 1964, *B. C. Templeton 10191* (RSA); Big Meadows, 1990 m, 27 July 1925, *J.B. Feudge 1242* (RSA); 2134 m, *N.C. Cooper 2886* (RSA); Cactus Flat, 1829 m, 25 June 1926, *P.A. Munz 10501* (RSA); Cactus Flat, August 1915, *F. Grinnell* (RSA); Camp Osceola, on the upper Santa Ana River, 1829 m, 21 July 1936, *E.R. Johnson* (NY); Coon Creek, Heart Bar State Park, 34°10′N, 116°45′W, 2286 m, 9 August 1992 , *S.D. White 599* (RSA); Cushenbury canyon, 1450 m, 5 May 1978, *R.F. Thorne 51874* (NY); 23 September 1927, *M. Jones* (RSA); Cushenbury Grade, 1219 m 9 July 1927, *J.T. Howell 318* (RSA); Fish Creek, 2743 m, 14 July 1924, *P.A. Munz 8497* (RSA); Santa Ana River, 1966 m, 22 October 1931, *C.B. Wolf* (NY); Foxesee Creek, 2438 m, 22 August 1920, *F.W. Peirson 1060* (NY); from Bear Lake to Holcomb Valley, 2134 m, 5 July 1930, *F.W. Peirson 9011* (RSA); Heart Bar campground, 34°10′N, 116°43′W, 2438 m, 17 July 1989, *B. Wagner* (RSA); Holcomb Valley, 3N10, 3N16, 7390 m, 12 & 13 July 1979, *R.F. Thorne 53493* (NY); Green Lead Mine road, 2195 m, 7 August 1931, *J. Ewan 4867* (NY); , T3N R1W sect. 34/26, 2134, 27 June 1979, *J. Strachan 2994* (NY); Johnson Grade, 1981 m, 5 July 1935, *M.B. Dunkle 4015* (NY); Baldwin Lake, 1951 m, 22 August 1932, *P.A. Munz 12707* (RSA); Lucerne Valley, OMYA's Crystal Creek Haul road, 34°20.5′N, 116°56.5 W, 1770 m, 27 August 1998, *S.D. White 7092* (NY); Marble Canyon, 34°20.5′N, 116°52.5′W, 1585 m, 26 August 1998, *S.D. White 7094, 7097* (RSA); near Bear Valley, September 1893, *T. Minthorn* (RSA); Nelson Ridge, south of Smarts Ranch, 34°16′.1″N, 116°45′37.1″W, 1951 m, 29 July 1998 , *S. Boyd 10259* (NY); Old Rose Mine, 2134 m, 9 October 1937, *P.A. Munz 14955* (NY); Onyx summit, 2450 m 30 August 1975, *C. Davidson 3234* (RSA); 34°11′13″N, 116°42′53″W, 2551 m, 27 March 1999, *S. Rhodes 9928* (RSA); Rose Mine, 2134 m, 21 October 1945, *H. Crooks 93* (NY); Santa Ana Canyon, 24 July 1906, *H.M. Hall 7549* (NY, RSA); Santa Ana River, 1920 m, 21 August 1922, *P.A. Munz 6147* (RSA); SE Terrace Springs and W of Arrastre Creek, 34°19′44″N, 116°45′58″W, 1463 m, 25 June 1998, *V. Soza 308* (RSA); Seven Oaks, July 1902, *C. Wilder 395* (NY); South Fork Public campground, 1981 m, 24 July 1947, *P.A. Munz 12053* (NY, RSA); South Fork, 1890 m, 26 July 1906, *J. Grimmell 307* NY; Sugarloaf Mountain, 2591 m, 22 July 1926, *P.A. Munz 10779* (RSA); 3 August 1932, *F.R. Fosberg 8617* (RSA);Warrens Well, 1280 m, 30 June 1938, *E.C. Jaeger* (NY); San Diego Co., Tantillas Mtns, 1875, *E. Palmer 304* (NY, RSA); Tulare Co., Chimney Creek Campground, opposite Lamont bench mark, 3 miles S of the BLM Chimney Creek Campground, 29 June 1985, *D.W. Mc Neil 3110* (NY); Kern Plateau, east of Long Valley, 1676–1859 m, 8 August 1967, *J.T. Howell* (NY); Kernville, head of Sand Canyon, T24S R36E sec29Se, 1981 m, 10 June 1986, *B. Ertter 6382* (NY).

Distribution. Inyo, Kern, Riverside, San Bernardino, San Diego, Cos., California and Clark and Tulare Cos., Nevada. 1219–2682 m (4000–8800 ft). Flowering from June–October.

Habitat. North facing slopes. Loose sand, limestone, or granitic soil. Found among pines and junipers.

Epithet etymology. The epithet refers to the thick leaves.

Salvia pachyphylla subsp. eremopictus R. Taylor subsp. nov. (Fig. 5) Arizona Rose Sage—TYPE: USA, Arizona: Navajo Co., 16.5 mi N of Interstate 40 on Hwy 87, just past mile marker 362; 2.5 mi N of Little Painted Desert State Park. UTM Zone 12 S, 550587E, 3893128N, 1676 m elev., 28 October 1999, *R. Taylor 04* (holotype, RSA; isotypes, ARIZ, ASC, ASU, NY).

Similis subsp. *pachyphylla*, sed differt floris internodis brevis, 6.5–15.5 mm longi, bracteae 3.5–9.2 mm lata.

FIG. 5. Illustration of *Salvia pachyphylla* subsp. *eremopictus*: A—flowering branch; B—longitudinal view of flower; scale bars = 1 cm.

Shrubs with well defined woody trunk, 35–50 cm tall, 40–150 cm wide. LEAVES spatulate, 2.0–4.4 cm long, 0.6–1.7 cm wide. INFLORESCENCE internodes 0.65–1.55 cm. FLOWERS 1.3–2.45 cm long. BRACTS many; 0.83–1.4 cm long; 0.35–0.92 cm wide; hairs on bracts 0.01 mm long; hairs on bract margins 0.01–0.03 mm. SEEDS 2.5–4 mm long, 1.5–2.5 mm wide.

Paratypes. U.S.A., Arizona. Apache Co., Petrified Forest National Monument, Chinde Mesa, 12 S 603424E 3892175N, 1804 m elev., 17 July 1998, *M. Hansen s.n.* (ASC); 2 September 2000, *R. Taylor 19* (ASC); Coconino Co., Meteor Crater, N-facing slope of crater, 35°01.923′N, 111°01.520′W, 1646 m elev., 28 October 1999, *R. Taylor 03* (ASC); 18 October 1998, *M. Hansen s.n.* (ASC); 26 May 1994, *J. Beasley s.n.* (ASC); 21 September 1998, *S. Hill 31025* (ASC); Navajo Co., Navajo Reservation, NW of Dilkon, 35°28′N, 110°19′W, 1937 m, 7 October 2001, *R. Taylor 26* (ASC, NY, RSA).

Distribution. Salvia pachyphylla subsp. *eremopictus* is known only from the southern Colorado Plateau in Apache, Coconino and Navajo Counties on Navajo reservation, National Park Service, State land, and private land at 1539–1937 m (5500–6356 ft) (Fig. 4). Flowering from (May) July–October usually after summer monsoon rains begin.

Habitat. Salvia pachyphylla subsp. *eremopictus* is found on barren north-facing slopes and washes on basalt and painted desert soils derived from Chinle shale. Found among juniper and salt bush.

Epithet etymology. The subspecific epithet refers to the "Painted-Desert" substrates derived from Chinle shale where historical populations of this taxon had been found. During this study three new populations were found on volcanic substrates adjacent to "Painted-Desert" formations.

Salvia pachyphylla subsp. meridionalis R. Taylor subsp. nov. Baja Rose Sage Illustration: Brittonia 34(2): 167. 1982.—TYPE: MEXICO, Baja California Norte, Sierra San Pedro Martir, La Encantada, rock hillsides about margin of meadow, 2100 m elev., 18 September 1930, *I. L. Wiggins and D. Demaree 48872* (holotype, RSA; isotypes, NY).

Similis subsp. *pachyphylla*, sed differt folia anguste, 5–14 mm lata.

Shrubs with well defined woody trunk, 30–45.5 cm tall, 61–120 cm wide. INTERNODES 1.4–3.35 cm. LEAVES linear to spatulate, 2.6–4.5 cm long, 0.5–1.4 cm wide. FLOWERS 1.5–2.1 cm long. BRACTS many; 0.97–1.9 cm long; 0.63–1.4 cm wide; hairs on bracts 0.01–0.015 mm long; hairs on bract margins 0.03–0.06 mm. SEEDS 3.0–4.0 mm long, 2.0–3.0 mm wide.

Paratypes. MEXICO, Baja California Norte. Observatoria UNAM, San Pedro Martir, 2830 m, 13 October 1985, *A. Gonzalez* (ASC); La Grulla, San Pedro Martir, 2286 m, 1926, *C.G. Abbott* (NY); UNAM Observatory, San Pedro Martir Mtns National Park, 1372 m, 5 August 1995, *H.D. Hammond 10844* (NY); UNAM Observatory, San Pedro Martir Mtns National Park, Vallecitos, 2590–2743 m, 1 September 1985, *J. Donahue 96055* (NY); Cerro Verado Blanco, San Pedro Martir, north-north west of the observatory, 31°3′N,115°9′W, 2345 m, 16 September 1998, *J. Rebman 5610* (RSA); Laguna Hanson, 9 July 1938, *M.B. Dunkle 5416* (RSA); Yerba Buena, Sierra San Pedro Martir, 31°00′N, 115°27′W, 16 August 1967, *Moran/ Thorne 14200* (RSA); La Corona, Sierra San Pedro Martir, 30°58′N, 115°35′W, 2000 m, 30 August 1963, *R. Moran 11272* (RSA); Rancho Mezquite, Sierra Juares, 32°18′N, 116°00′W, 1450 m, 3 September 1966, *R. Moran 13446* (RSA); Arroyo Copal, Sierra San Pedro Martir, 31°04′N, 115°28′W, 2550 m, 24 August 1968 , *R. Moran 15436* (RSA); Laguna Hanson, Sierra de Juares, Constitucion National Park, 32°02.5′N, 115°55′W, 1610 m, 15 September 1983, *R.F. Thorne 57116* (RSA); Sierra Juarez, Estado de Baja California,

3 miles east of Laguna Hanson, 32°02′N, 115°52′W, 26 July 1994, *J. Rebman 2839* (NY);14 miles south of La Rumerosa, 32°21′N, 116°00′W, 29 June 1962, *R. Moran 9805* (RSA); La Corona de Abajo, Parque Nacional Sierra San Pedro Martir, 2080 m, 27 August 1988, *R. Noyes 638* (RSA); Cerro Botella Azul, Sierra San Pedro Martir, 19 July 1988, *S. Boyd 2643* (RSA); Vallecitos, Sierra San Pedro Martir, 1 mile S of La Tasajera, 20 July 1988 , *S. Boyd 2725* (RSA); Vallecitos, Sierra San Pedro Martir, 2456 m, 21 September 1930 , *Wiggins & Demaree 4971*(NY, RSA); La Encantada, Sierra San Pedro Martir, 30°55′N, 115°24′W, 2200 m, 19 August 1967, *Moran & Thorne 14370* (RSA); La Encantada, *Wiggins & Demaree 4887* (NY, RSA); La Encantada, Sierra San Pedro Martir, 2200, 18 September 1930, *Wiggins & Demaree 4892* (NY, RSA); Yellow pine belt, between Ojos Negros and Neji Rancho, 16 September 1929, *Wiggins & Gillespie 4137* (NY, RSA).

Distribution. Salvia pachyphylla subsp. *meridionalis* is distributed in the Sierra San Pedro Martir and Sierra Juarez from 32°00′N, 116°00′W to 30°25′N, 115°30′W at 1372–2830 m (4500–9284 ft) (Strachan 1982, Fig. 2). Flowering from June–August.

Habitat. Salvia pachyphylla subsp. *meridionalis* is found on north-facing rocky slopes derived from coarse sand and granitic soil. Found among pines.

Epithet etymology. The subspecific epithet refers to the southern-most distribution of this taxon.

Acknowledgments

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THE EVOLUTION OF PINK: MORPHOLOGICAL AND GENETIC VARIATION AMONG THREE *LITHOPHRAGMA* (SAXIFRAGACEAE) SPECIES

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ABSTRACT

Prior molecular work using ITS and chloroplast sequence data revealed that the endemic *Lithophragma trifoliatum* and the broad-ranging *L. parviflorum* form a tight clade with a third species, *L. affine*. We used AFLPs to assess the fine scale relationship of these three species from populations where their distributions overlap in northern California. Our results revealed two groups of *L. trifoliatum*, one nested within a group of *L. affine* and *L. parviflorum* and the other grouped with other populations of *L. parviflorum*, contrary to predictions based on plant morphology alone. The morphological pattern was not supported by the molecular data, suggesting that pink flowers evolved more than once, concurrently with other floral traits such as size and nectary length. It is also possible that this pattern is due to recent evolution or gene flow between the two color morphs. The possible ecological importance of these differences in floral traits (e.g., for pollination) warrants further study, as well as the extent to which these populations are reproductively isolated.

Key Words: Amplified fragment length polymorphisms (AFLPs), endemic, floral traits, genetic variation, *Lithophragma*, Saxifragaceae.

Floral morphology has been found to be important in reproductive success (e.g., Galen 1989; Herrera 1993; Guitian et al. 1997), pollinator specialization (Muchhala 2003) and isolation between plant species (e.g., Bradshaw Jr. et al. 1998; Ellis and Johnson 1999; Fulton and Hodges 1999). Floral traits may dictate reproductive success by mediating attractiveness to pollinators. In this way, individual pollinators may exert strong directional selection for particular floral syndromes (Campbell et al. 1997). In part because they often play a role in reproductive isolation, floral traits are also used to differentiate closely related species. Yet, are these floral traits meaningful in explaining the genetic relatedness among populations and species? Floral morphology alone can be phylogenetically deceptive due to convergent evolution and the gene flow and hybridization that can result from shared pollinators.

The processes of diversification and speciation remain important problems in evolutionary biology because species arise through many genetic mechanisms and their relative importance among different taxa is unresolved (Hewitt 2001). Diversification in plants is particularly intriguing because they may speciate through hybridization and exhibit reticulate evolution. Incomplete reproductive isolation can limit diversification, but it also may maintain a greater range of floral morphologies, as intermediate morphotypes would be maintained due to gene flow and hybridization. Hybridization can result in genetic variation, which provides the raw material for rapid adaptation and can play an important role in evolutionary diversification (Rieseberg 1997; Arnold et al. 1999; Rieseberg et al. 2000).

The genus *Lithophragma* (Saxifragaceae) provides an opportunity to evaluate how floral morphology and hybridization contribute to the diversification of plant taxa. The genus has ten named species that differ in floral morphology, hybrid history and geographic range (Taylor 1965). Three of the species within this genus, *L. affine* A. Gray, *L. parviflorum* (Hook) Torrey & A. Gray, and *L. trifoliatum* Eastw. form a tight clade and represent the extremes in geographic distributions within the genus (Taylor 1965; Nicholls and Bohm 1984; Soltis et al. 1992; Kuzoff et al. 1999). Hybridization has been suggested among these three species (Taylor 1965). In addition, results from a phylogeny based on internal transcribed spacer (ITS) sequences of ribosomal DNA showed these species as a paraphyletic group (Kuzoff et al. 1999). The authors thought the most compelling reason for this is that the putative species are not distinct lineages. In the literature, there is disagreement regarding their specific status: Taylor (1965) lists them as three separate species, while the Jepson Manual (Hickman 1996) lists two species, *L. affine* and *L. parviflorum* vars. *parviflorum* and *trifoliatum*.

Although existing molecular studies have shown these three species to be genetically very similar, they differ in several morphological traits, including some (i.e., floral scent and color; see Table 1) that are unique

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TABLE 1. SUMMARY OF SPECIES DESCRIPTIONS. INFORMATION IN TABLE FROM THE JEPSON MANUAL (HICKMAN 1993) AND TAYLOR (1965). The Jepson Manual (Hickman 1993) lists *L. trifoliatum* as *L. parviflorum* var. *trifoliatum* and *L. parviflorum* as *L. parviflorum* var. *parviflorum*.

Species	Flower color	Floral shape	Leaf shape	Floral scent	Ploidy (2n)	Distribution
L. affine	White	Hypanthium obconic, inflated above	Shallowly lobed	none	14, 21, 28	Coastal mountains of CA, a few specimens in outer central Sierra Nevada foothills. Open well-drained grassy clearings or open bluffs in oak or coniferous-oak woodlands from sea level to 2150 m
L. parviflorum	Generally white, some pink	Hypanthium long-obconic, 2× longer than wide	Deeply lobed	none	14, 21, 28, 35	W. NA (BC, WA, ID, MT, OR, WY, SD, CA, NV, UT, CO); Habitat extremely variable, seacoast bluffs to open gravelly prairielands, to subalpine regions up to 3050 m elevation
L. trifoliatum	Pink	Hypanthium long-obconic, 3–4× longer than wide	Deeply lobed	fragrant	28	Restricted to western slope of the Sierra Nevada, with center in Butte Co., CA. In igneous-derived scabland in oak-coniferous woodland from 60–600 m elevation

within the genus. Northern California is the only place in the range of this genus where plants with pink flowers occur. Along with these pink flowers are other unusual traits for this genus, such as much longer petals and hypanthia (see Table 1). There are also populations that have larger white flowers, resembling *L. parviflorum*, but that have leaf morphology more similar to *L. affine*. Populations with mixed traits (generally labeled *L. parviflorum*) in this region led Taylor (1965) to conclude that there was hybridization in this region.

This species complex provides an opportunity to study two central questions regarding the diversification of plant taxa: 1) Do these populations of putative species differ consistently in the floral traits that are used to distinguish the species? 2) Do patterns of floral morphology inform our understanding of phylogenetic relationships among these species? Specifically, does the unique pink color correlate with other floral traits that differ consistently among species? If the pink flowers have evolved only once and are an important reproductive isolating mechanism among these species, we expect the populations with pink flowers to be more closely related to each other than to populations with white flowers and for there to be limited gene flow between populations of different flower color.

MATERIALS AND METHODS

Geographical Distribution of *Lithophragma*

Lithophragma (Saxifragaceae) is an herbaceous perennial genus with a broad geographical distribution from southern California to southern British Columbia and from the west coast of North America to South Dakota (Taylor 1965). The genus is thought to have originated within California (Taylor 1965), where most taxa and the most basal taxa occur (Taylor 1965; Soltis et al. 1992; Kuzoff et al. 1999).

Molecular data indicate that *L. affine*, *L. parviflorum*, and *L. trifoliatum* are so similar that the limits of the species are uncertain with respect to both the chloroplast and nuclear markers that have been used (Soltis et al. 1992; Kuzoff et al. 1999). These three species may, therefore, not be distinct lineages. Nonetheless, these taxa differ in a variety of morphological traits and geographical distribution, with more differentiation occurring among populations and species in California (near the purported center of the distribution) than in more northerly populations.

Lithophragma affine is primarily restricted to the coastal mountains of California from Humboldt County to Santa Barbara County (Taylor 1965), but a few specimens have been found in the foothills of the central Sierra Nevada, in Tuolumne, Stanislaus, and Amador counties (CalFlora Occurrence Database; UC, Berkeley Jepson Herbarium). Taylor (1965) described *L. affine* as very polymorphic due to environmental variability and population isolation caused by the topography of the region.

Lithophragma parviflorum is the most widely distributed species in the genus. It ranges from southern California to southern British Columbia and from the west coast of North America to South Dakota. Across its wide range, *L. parviflorum* shows great morphological variation.

Lithophragma trifoliatum has the narrowest distribution in the genus and is restricted to the western slope of the Sierra Nevada. Taylor (1965) considered this species closely related to *L. parviflorum*. His data indicated that this species represented a sterile derivative of *L. parviflorum* that was persisting through vegetative reproduction in a small geographic area. (However, field-collected seeds have germinated in the greenhouse (Hufft unpublished data), but the extent of their viability across all populations is not known.) More recent phylogenies have shown that *L. trifoliatum* is part of the *L. parviflorum/affine* clade, but its exact relation to the other two species is not known (Soltis et al. 1992; Kuzoff et al. 1999).

Sampled Populations

The distributions of all three species, which overlap in northern California, provide an opportunity to study local phylogeographic patterns of this complex, which have been unresolved in the larger scale phylogeographic work that has been done on this genus. Sixteen populations, along with several roadside collections, were located in spring 2001 and 2002 in Mendocino, Tehama, Butte, Plumas, and Lassen Counties (Fig. 1). Populations were chosen within the zone of overlap in northern California that represent the morphological diversity of the three species (Table 2). Populations were identified to species based on the floral characteristics that define them in Jepson (Hickman 1994) and verified by a local expert, Vern Oswald. Plants were haphazardly selected and were chosen at least two meters from the nearest plant used to ensure that they were distinct individuals and not growing from the same underground bulbils.

Floral Morphology

Although these species have similar floral structures, relative to other species in the genus (Kuzoff et al. 2001), variation in floral traits are used to distinguish among the three species (Taylor 1965; Hickman 1996). Nine morphological traits were measured on field-collected flowers: average petal length, average petal width, corolla gap, floral length, tip to nectary, short angle, average nectary depth, nectary length, and average diaganol (Fig. 2). The second flower from each plant was collected from all study sites (Table 2) and stored in 70% ethanol. Floral traits were measured using a microscope (Wild M8 microscope) fitted with an ocular micrometer. For these nine traits, 144 flowers were analyzed from 14 populations (Table 2) using Principal Components Analysis (PCA).

Flower color was not included in the analysis because it is not a quantitative trait and only one color (white or pink) occurred within a population. Instead, flower color was used as a grouping variable in the various analyses to determine its usefulness in distinguishing among the species.

We used discriminant analysis to determine if flower color, species, or molecular group (based on AFLP data, see below) better differentiated these individuals based on floral morphology (SAS 6.12 1996). Half of the samples in each group were randomly selected to create the discriminant function, with the other half used to test the model. The proportion of test samples classified correctly provided a quantitative measure of the ability of each grouping variable to accurately distinguish among these individuals. Estimates of pairwise population morphological distances were calculated with discriminant analysis (SYSTAT 10.2 2002) for comparison with estimates of genetic distance (see below).

Pollinator Observations

We performed pollinator observations at six sites in spring 2002 (1 *L. affine*, 1 white *L. parviflorum*, 1 pink *L. parviflorum*, and 3 *L. trifoliatum*). We chose plants haphazardly and observed all plants within a 1-m quadrat (number of plants per observation=1–13) for 30 min. We performed a total of 112 observation periods (15 *L. affine*, 61 *L. parviflorum*, and 35 *L. trifoliatum*). We recorded the number of flowers within a quadrat, the number and identity of pollinator visitors and the number of flowers visited.

Amplified Fragment Length Polymorphisms (AFLPs)

Gene flow within and among populations and patterns of relatedness among individuals and populations was evaluated using genetic fingerprinting (amplified fragment length polymorphisms [AFLPs; Vos et al. 1995] that are predominantly nuclear). DNA was extracted using the method from Doyle and Doyle (1987). Following standard protocols, AFLPs were analyzed (Applied Biosystems manuals 1997). A total of 158 individuals from 16 populations (Table 2) were scored for the presence of 216 markers from two ABI AFLP primers, CAT-ACT (blue) and CAG-AAG (green). Data were analyzed with an AMOVA using ARLEQUIN (Schneider et al. 2000), a Principle Coordinate Analysis (PCoA) using the R Package (Casgrain 2004) and UPGMA using PAUP 4.0b10 (Swafford 2001) and visualized in TreeView (Page 2001). Pairwise population differences were calculated, a one-way AMOVA was performed to measure among population variation and a hierarchical AMOVA was performed to partition the variance into species and floral color effects. The relationship between floral morphol-

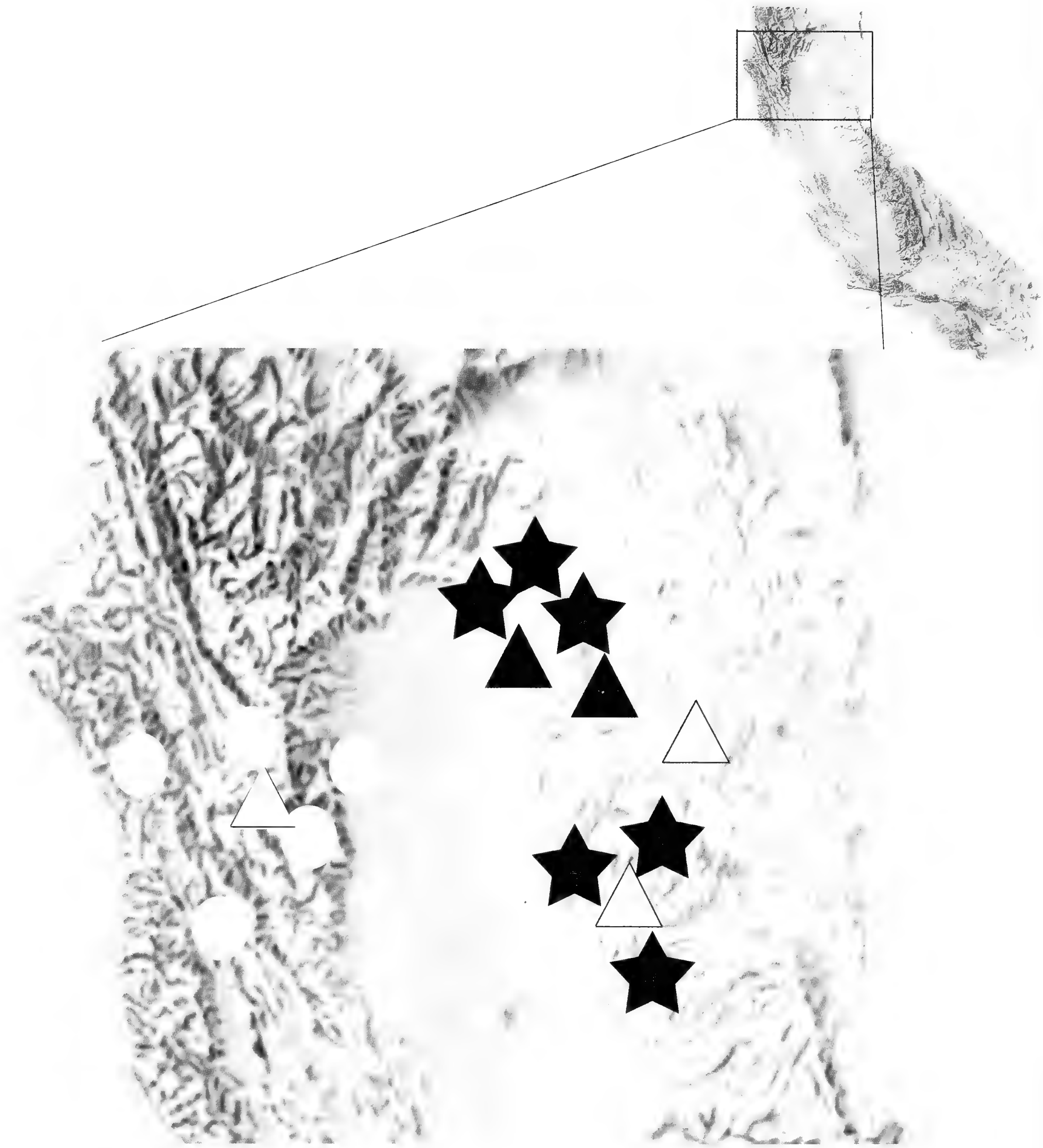

FIG. 1. California field sites, as numbered in Table 2. White circles = *L. affine*, white triangles = white-flowered *L. parviflorum*, black triangles = pink-flowered *L. parviflorum*, and black stars = *L. trifoliatum*.

ogy and genetic relatedness was first assessed by comparing the output of the PCA and PCoA. The quantitative floral morphology data and AFLP data were then statistically compared using a regression of the AFLP genetic distances and the floral morphology distances, to test for a positive relationship between genetic and floral distances from the discriminant analysis. A log transformation was performed on floral distances to normalize data prior to performing the linear regression.

RESULTS

Floral Morphology

Results of the PCA suggest that populations with pink flowers (*L. parviflorum* and *L. trifoliatum*) can be distinguished from populations with white flowers (*L. parviflorum* and *L. affine*) to some degree but the measured floral traits exist along a continuum (Fig. 2). Axis 1 and Axis 2 explained 46% and 23% of the variation, re-

TABLE 2. SPECIES, FLOWER CCOLOR AND NUMBER OF SAMPLES UUSED FOR THE MORPHOLOGICAL AND GENETIC ANALYSES FOR EACH POPULATION. [a] Not used in AMOVA analyses.

Population	Species	Flower Color	Flower Count	AFLP count
1. Alder	Affine	White	1	6
2. Big Oak	Affine	White	14	10
3. Hwy101	Affine	White	6	1[a]
4. Mendocino1	Affine	White	9	11
5. Mendocino2	Affine	White	5	10
6. Feather Falls	Parviflorum	White	10	14
7. Hwy70	Parviflorum	White	19	10
8. Plasket Meadows	Parviflorum	White	0	2
9. Dye Creek	Parviflorum	Pink	1	9
10. Hogsback	Parviflorum	Pink	60	25
11. Forbestown	Trifoliatum	Pink	0	3
12. Hog Lake	Trifoliatum	Pink	1	12
13. Hwy 36	Trifoliatum	Pink	0	3
14. MilsapBar	Trifoliatum	Pink	3	17
15. North Table MT	Trifoliatum	Pink	10	14
16. Shingletown	Trifoliatum	Pink	0	11
		Total	**139**	**158**

spectively (Table 3). Most populations did not fall out as tight clusters (data not shown). The white and pink flowered individuals separate out mainly along Axis 2. The traits that have the strongest influence on axis 2 are length of nectary (with an eigenvector value of 0.556), nectary depth (0.443) and corolla gap size (0.519). Flower color was a very good grouping variable in the DFA, with high classification rates for both colors (Table 4). Although, *L. parviflorum* and *L. affine* also showed high classification rates, *L. trifoliatum* proved to be a very bad grouping variable, with the majority of *L. trifoliatum* individuals being classified as *L. parviflorum* (Table 4). The molecular groups had a higher total misclassification of individuals (35%) than either color (13%) or species (26%).

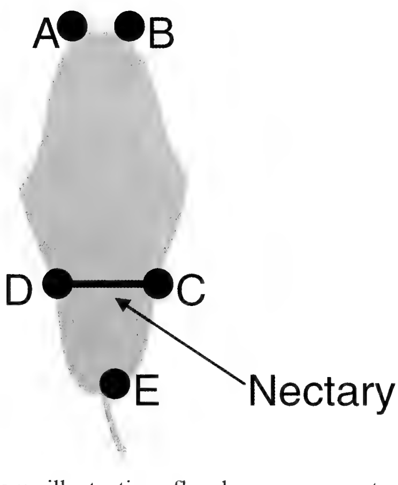

FIG. 2. Diagram illustrating floral measurements. Corolla gap = distance between A and B, flower length = midpoint of A and B to E, tip to nectary = midpoint of A and B to the midpoint of C and D, short angle = B to C, average diagonal = A to C and B to D, average nectary depth = height of nectary, and nectary length = C to D.

Pollinator Observations

We recorded 128 insects visiting 324 flowers. These preliminary observations revealed that although the pink populations received more visits (1.15 pollinators/observation period vs. 0.56 for white populations), generalists (Bombyliid flies and solitary bees) were visiting all of the plants, indicating the possibility of gene flow between the color morphs. Unlike previous studies of *L. parviflorum* (Thompson and Pellmyr 1992; Thompson 1999; Thompson and Cunningham 2002), the specialist *Greya politella* was found at only one site (6. Feather Falls).

AFLPs

The results of the PCoA are shown in Figure 4, with individuals labeled by species and flower color. *Lithophragma trifoliatum* is split into two groups along axis 2, and the majority of samples with pink flowers are clumped along the same half of axis 1. Additionally, the AFLP results can be seen in the UPGMA phenogram (Fig. 5). Although, populations mostly group together, there is very low resolution of the relationships among populations. Population 15 (North Table Mountain) appears to be the most derived. Although not strongly supported, Population 14

TABLE 3. RESULTS OF PRINCIPAL COMPONENT ANALYSIS OF FLORAL MORPHOLOGY. Variance extracted on the first three components (a) and eigenvectors of floral characters (b).

A.

Component	Eigenvalue	% of Variance	Cum.% of Var.
1	4.181	46.450	46.450
2	2.055	22.834	69.285
3	0.818	9.085	78.369

B.

Character	Eigenvector 1	Eigenvector 2	Eigenvector 3
Average petal length	−0.3814	−0.1771	0.1858
Average petal width	−0.3831	−0.1858	0.1583
Corrolla gap	−0.1280	0.5185	−0.5339
Floral length	−0.3623	0.1151	0.1068
Tip to nectary	−0.4211	−0.1961	−0.0721
Short angle	−0.4184	−0.2448	−0.0660
Average nectary depth	−0.1032	0.4426	0.7313
Nectary length	−0.1388	0.5561	0.0728
Average diagonal	−0.4216	0.2202	−0.3070

(Milsap Bar) is more closely related to the two geographically closest populations (6. Feather Falls and 7. Hwy 70) than to other *L. trifoliatum* populations.

The one-way AMOVA results revealed significant genetic differentiation among populations, with 35.9% of the variation partitioned among the populations. The pairwise genetic distances are given in Table 4. Of the 105 comparisons, 6 were not significant. A nested ANOVA of genetic distances grouped by comparisons within species versus comparisons among species revealed that there was no difference between within versus among species comparisons (F-ratio = 0.686, df = 1, P = 0.409), meaning that overall distances between populations of different species were not different from distances of populations of the same species. However, there were significant differences in the comparisons of distances among species and the distances within species (F-ratio = 2.898, df = 4, P = 0.024), with pairs involving *L. trifoliatum* having the largest within species distances and those involving *L. affine* having the smallest. The *L. trifoliatum-L. parviflorum* group was the largest among species distance. However, distances between populations of the same color were more similar than populations of different color (Pooled Variance t = 2.757, df = 151, P = 0.007). No relationship was found between the pairwise genetic and morphological distances (b = −0.022, P = 0.222, adjusted r^2 = 0.007). The power of this test to detect a positive slope as small as 0.05 was 0.77.

DISCUSSION

Currently defined species within this group (Hickman 1996; Taylor 1965) do not appear much differentiated by floral morphology. The traits that seem to be most important in separating individuals in the PCA are corolla gap, nectary length and nectary depth, all traits that could be important in pollinator preference (Campbell et al. 1997; Fulton and Hodges 1999). In addition, floral color can be an important cue in pollinator discrimination (Wilson and Stine 1996) and also appears to distinguish two main groups of individuals when they are plotted onto the first two principal components. However, the three species are not segregated into discrete groups by the principal components. The predominance of generalist pollinators in this region would suggest that other, possibly neutral mechanisms, are maintaining floral variation. It has been hypothesized that diversity of ovary position in species of *Lithophragma* may be the result of modifications in one or a few genes (Kuzoff et al. 2001). This could also be the cause of the variation in other floral traits, like those measured here.

Using genetic markers to analyze these groups, the three species clump together indicating they are closely related. The degree of overlap suggests these are not distinct species. Location is important (i.e., populations clump together indicating individuals within a population are closely related), but flower color also has some genetic component (i.e., clumping of pink and white flower color along Axis 1, Fig. 4). Larger genetic distances between *L. trifoliatum* populations help explain the separation of this species into two groups in the PCoA. This could indicate more variation within populations or multiple lineages. This was also supported in the discriminant function analysis of morphological traits, where *L. trifoliatum* was not found to be a viable group. Flower color was not as good a grouping variable for the genetic relationships as it was for the floral morphology (see separation of pink

TABLE 4. DISCRIMINANT FUNCTION ANALYSIS OF FLORAL MORPHOLOGY GROUPED BY SPECIES, COLOR AND MOLECULAR GROUP. Molecular groups were based on AFLP results: Group 1 = 1.Alder, 3.Hwy101, 7.Hwy70; Group 2 = 6.Feather Falls, 14.Milsap Bar; Group 3 = 2.Big Oak, 4.Mendocino1, 5.Mendocino2; Group 4 = 15.North Table Mountain; Group 5 = 9.Dye Creek, 10.Hogsback, 12.Hog Lake. The total-sample standardized canonical coefficients are shown, along with the percent classifications for the testing samples. [a]Total error=26.05%. [b]Total error=13.25%. [c]Total error = 35.38%.

Total-Sample Standardized Canonical Coefficients

Species:	Petal length	Petal width	Corrola gap	Flower length	Tip to nectary	Short angle	Nectary depth	Nectary length	Diagonal
CAN1	0.301	−0.120	−0.104	0.898	1.748	−1.99	0.173	−1.050	0.381
CAN2	−0.991	0.683	1.003	0.925	−5.547	5.713	−0.464	−0.027	−0.299
Color:									
CAN1	−00.015	0.044	−.492	0.838	0.346	0.474	−0.196	−.0.737	−0.292
Molecular:									
CAN1	0.337	0.240	−0.173	0.848	−0.177	0.765	0.001	−1.271	0.030
CAN2	0.824	−0.996	0.653	0.687	0.657	−0.914	0.398	−0.152	0.046
CAN3	−00.790	0.371	−0.033	1.233	1.502	−1.225	−0.391	0.864	−0.915
CAN4	0.281	0.755	0.290	−0.332	−0.085	−0.635	−0.410	−0.109	0.802

Percent Classified into Species:

From Species:	*L. parviflorum*	*L. trifoliatum*	*L. affine*	% error[a]	No. of samples
L. parviflorum	84.09	13.64	2.27	15.91	44
L. trifoliatum	57.14	28.57	14.29	71.43	7
L. affine	31.25	0	68.75	31.25	16

Percent Classified into Color:

From color:	Pink	White	% error[b]	No. of samples
Pink	91.89	8.11	8.11	37
White	19.35	80.65	19.35	31

Percent Classified into Molecular Group:

From group:	1	2	3	4	5	% error[c]	No. of samples
1	46.15	23.08	15.38	0	15.38	53.85	13
2	33.33	33.33	33.33	0	0	66.67	6
3	21.43	7.14	64.29	0	7.14	35.71	14
4	0	0	0	0	100	100.00	5
5	0	0	6.67	3.33	90.00	10.00	30

TABLE 5. PAIRWISE POPULATION DIFFERENTIATION EXPRESSED BY Φ_{ST} (EXCOFFIER ET AL. 1992). Bold values are not significant. Population names refer to population number and species (Aff = *L. affine*, Par = *L. parviflorum*, Tri = *L. trifoliatum*). For *L. parviflorum*, flower color is also noted (P = pink, W = white).

	1Aff	2Aff	4Aff	5Aff	6ParW	7ParW	8ParW	9ParP	10ParP	11Tri	12Tri	13Tri	14Tri	15Tri
2Aff	0.412													
4Aff	0.391	0.202												
5Aff	0.316	0.236	0.218											
6ParW	0.545	0.429	0.263	0.404										
7ParW	0.296	0.296	0.198	0.265	0.188									
8ParW	0.314	0.365	0.279	0.337	0.508	**0.105**								
9ParP	0.499	0.350	0.224	0.344	0.369	0.253	0.464							
10ParP	0.397	0.286	0.169	0.245	0.213	0.185	0.317	0.094						
11Tri	0.463	0.359	0.125	0.327	**0.062**	**0.062**	**0.271**	0.335	0.147					
12Tri	0.601	0.443	0.351	0.417	0.486	0.334	0.600	0.354	0.213	0.552				
13Tri	0.423	0.323	0.128	0.268	0.409	0.158	**0.257**	0.185	**0.036**	0.338	0.326			
14Tri	0.579	0.476	0.348	0.462	0.259	0.258	0.569	0.502	0.306	0.328	0.568	0.525		
15Tri	0.649	0.488	0.369	0.487	0.561	0.424	0.660	0.449	0.295	0.590	0.626	0.528	0.613	
16Tri	0.524	0.299	0.237	0.314	0.408	0.301	0.514	0.241	0.178	0.440	0.363	0.271	0.504	0.456

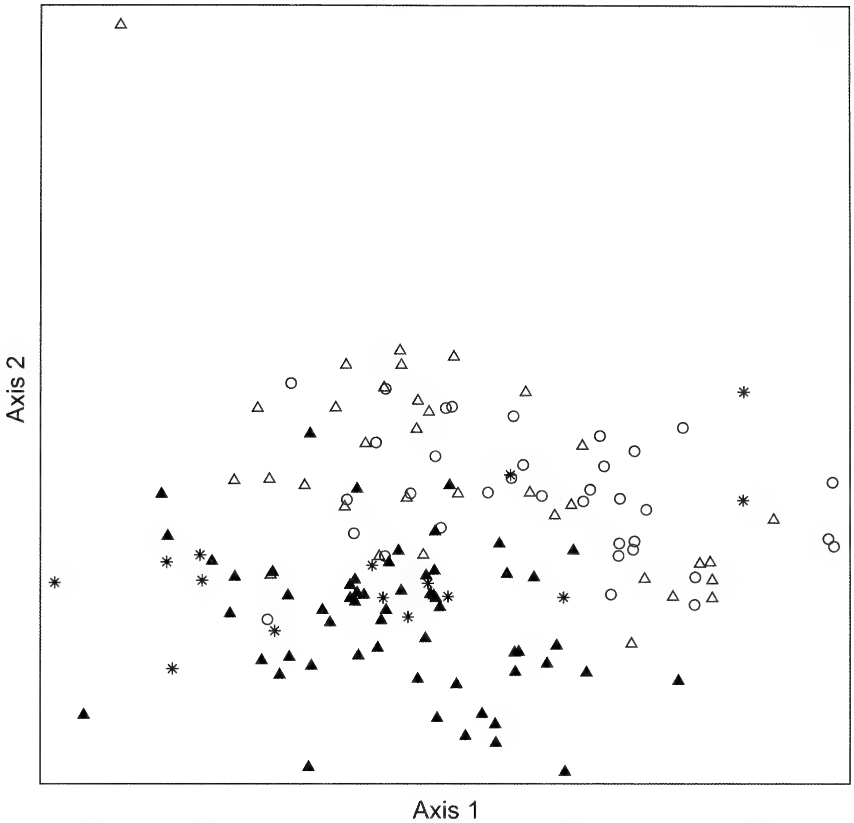

FIG. 3. Principal Component Analysis of floral morphology data labeled by species and flower color. ○ *L. affine*, white; △ *L. parviflorum*, white; ▲ *L. parviflorum*, pink; * *L. trifoliatum*, pink.

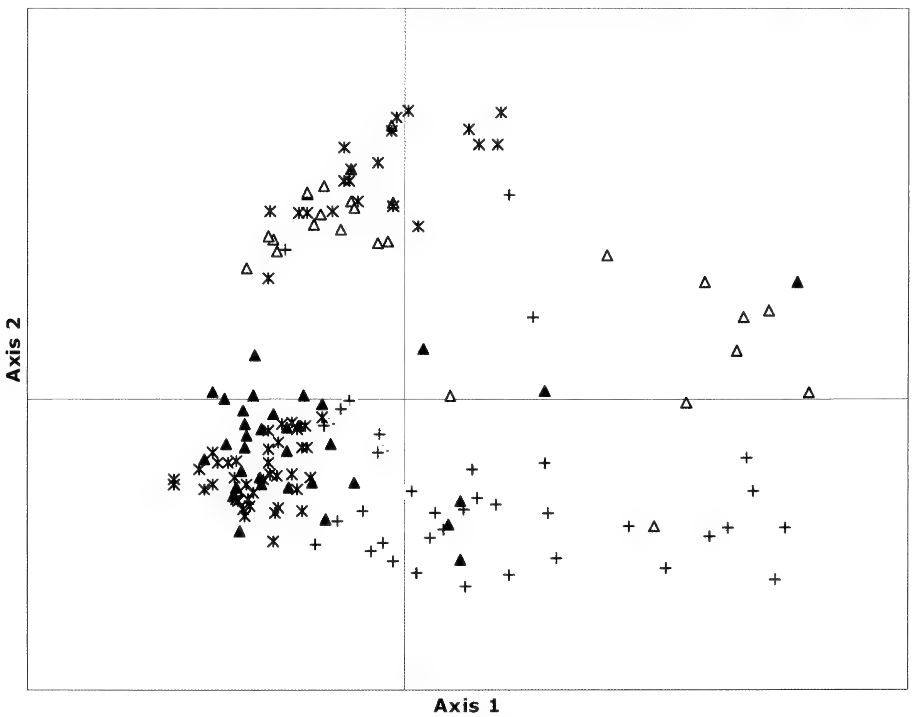

FIG. 4. Principal Coordinate Analysis of AFLP data. + *L. affine*, white; △ *L. parviflorum*, white; ▲ *L. parviflorum*, pink; ✳ *L. trifoliatum*, pink.

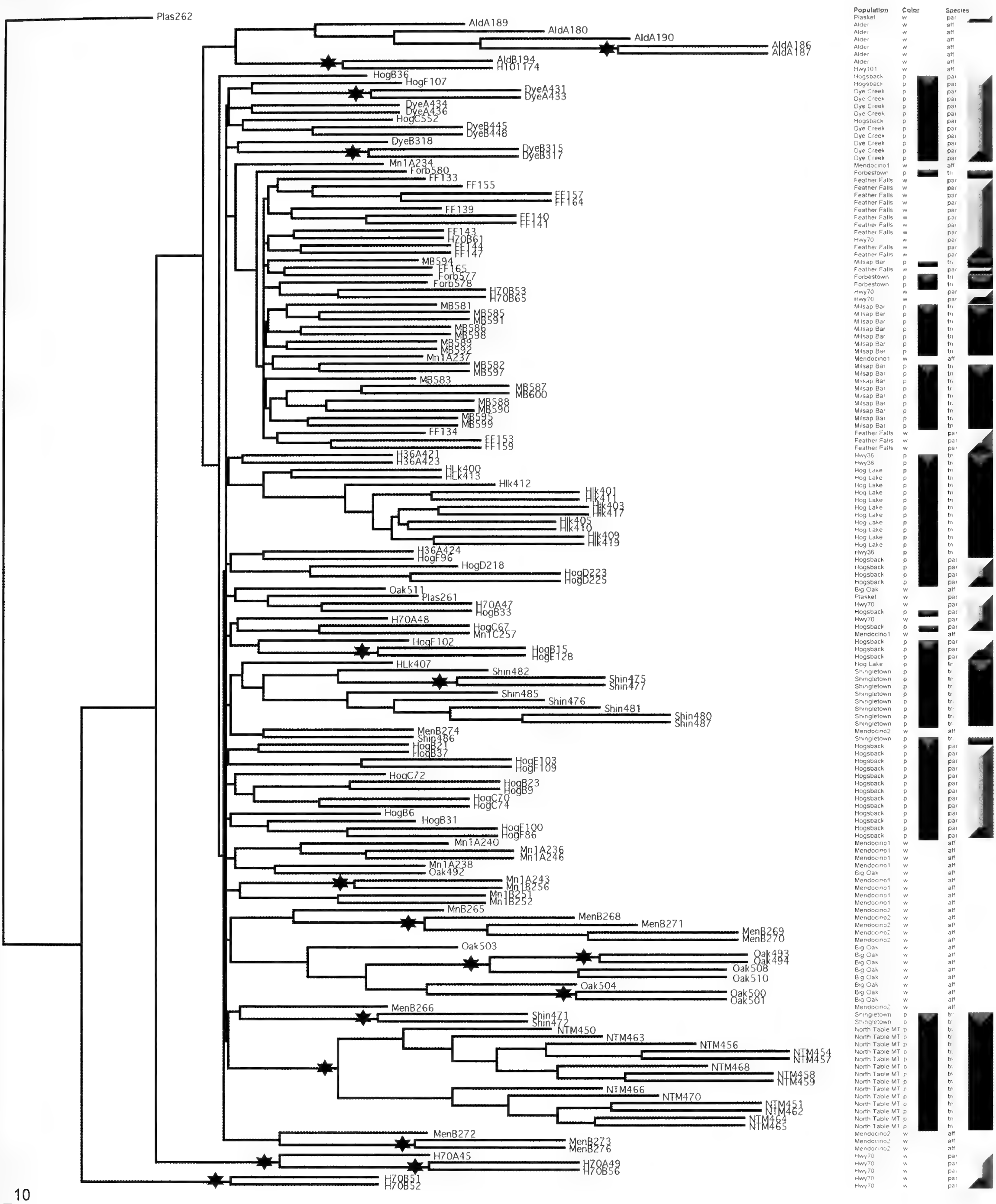

FIG. 5. UPGMA phenogram of AFLP data. Bars to the right of figure indicate flower color (black = pink) and species (black = *L. trifoliatum*, gray = *L. parviflorum*). White flowers and *L. affine* are indicated by spaces between the bars. * mark bootstrap values greater than 70%.

into two main groups in Fig. 4, and lack of association in Fig. 5). This could be because the pink morph has evolved more than once, it evolved recently or there is gene flow between the two color morphs. If pollinators were a strong isolating mechanism we would expect less overlap among the species and between individuals of different flower color in the AFLP data, indicating less gene flow. The lack of a relationship found between the molecular and morphological

data could be due in part to shared pollinators. However, it is also possible that very strong selection has resulted in the morphological divergence we see despite the molecular evidence of gene flow. The floral traits are thought to be genetically inherited, but a common garden experiment is necessary to separate the environmental component that could be responsible for some of the variation in the data (although no obvious habitat variation is known among the populations).

The three taxa studied here differ in the size of their geographic ranges, which might influence the morphological variation observed, as you would expect species with larger ranges to have more morphological variation due to the increased environmental variation across their range. An additional aspect of this work was to identify genetic and ecological differences between a narrow endemic and its broad ranging relatives. It is expected that rare plants have low phenotypic variability (Kruckeberg and Rabinowitz 1985), but this is not always the case (Guitian et al. 1997). Given the narrow distribution of *L. trifoliatum* relative to its two sister species studied here, the expectation would be for it to show less variation in phenotypic traits than *L. affine* and *L. parviflorum*. However, all three species show similar amounts of variation for each individual trait measured (data not shown). It is possible that the morphological variation seen over the range of this clade is not due to differences among three species, but rather is just variation within one or two species. In agreement with previous work in this system, this research shows there is strong evidence that these are not three distinct lineages. The addition of the morphological data also supports previous molecular work that *L. trifoliatum* may not be a true, distinct species.

In order to better understand why these species show more variation in morphology than at neutral molecular markers, the relative importance of selection and local adaptation must be determined. More pollinator observations, preference trials and estimates of pollinator travel distance will help us better understand the role of biotic selection on these species. Sorting out the amount of gene flow and the mechanisms responsible for the maintenance of floral variation will also aid our understanding of the roles of selection versus drift in creating this variation in floral morphology. Exploring these diversification mechanisms will give us insight into their role in creating and maintaining biodiversity on a broader scale.

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ADDITIONS TO THE VASCULAR FLORA OF WASHINGTON FROM A BIODIVERSITY STUDY ON THE HANFORD NUCLEAR RESERVATION

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ABSTRACT

During a three-year botanical inventory of the Hanford Nuclear Reservation in south-central Washington, we located three previously undescribed entities (*Astragalus conjunctus* S. Watson var. *rickardii* Welsh, K.A. Beck, and Caplow, *Eriogonum codium* Reveal, Caplow, and K.A. Beck, and *Physaria douglasii* (S. Watson) O'Kane and Al-Shehbaz subsp. *tuplashensis* (Rollins, K.A. Beck, and Caplow) O'Kane and Al-Shehbaz, four species new to Washington (*Cistanthe rosea* (S.Watson) Hershk., *Gilia leptomeria* A. Gray, *Loeflingia squarrosa* Nutt., and *Myosurus clavicaulis* M.E. Peck), and one previously described species that had generally gone unnoticed by the American botanical community (*Festuca washingtonica* E.B. Alexeev). The botanical inventory was a part of the Hanford Biodiversity Project, which was funded by the Department of Energy and administered by The Nature Conservancy of Washington.

Key Words: Hanford Nuclear Reservation, *Astragalus conjunctus* var. *rickardii*, *Eriogonum codium*, *Physaria douglasii* subsp. *tuplashensis*, *Cistanthe rosea*, *Gilia leptomeria*, *Loeflingia squarrosa*, *Myosurus clavicaulis*, *Festuca washingtonica*.

The 1450 km^2 Hanford Nuclear Reservation (Hanford Site) is located in Benton, Grant, and Franklin Counties in south-central Washington (Fig. 1). It was acquired in 1943 by the U.S. Government for the production of weapons-grade plutonium, and it has been administered by the U.S. Department of Energy (DOE), or its predecessors. Portions of the Hanford Site have also been administered by the U.S. Fish and Wildlife Service (FWS) and the Washington State Department of Wildlife. The majority of the Hanford Site has been closed to the public and to grazing and agriculture since 1943.

In the last two decades, the mission of the Hanford Site has changed to nuclear waste clean-up, environmental restoration, research and development. In 1992, the DOE and The Nature Conservancy of Washington (TNC) entered into a Memorandum of Understanding that called for a cooperative and coordinated inventory of plants, animals, and ecologically significant areas of the Hanford Site. The Hanford Biodiversity Project began in 1994 and continued through 1998 (Soll et al. 1999). The authors conducted the botanical portion of the Biodiversity Project from 1994 through 1997. A description of previous botanical work and a checklist of vascular plant collections from the Hanford Site is in Sackschewsky and Downs (2001).

In 1999, the Hanford Reach of the Columbia River was designated a Wild and Scenic River. In 2000, President Clinton declared 78,780 ha of the Hanford Site the "Hanford Reach National Monument" and placed administration of the National Monument under the jurisdiction of the FWS. The new Monument includes the Hanford Reach of the Columbia River, the lands north of the Columbia River, and the 31,080 ha Fitzner-Eberhardt Arid Lands Ecology Reserve (ALE) (Fig. 1).

The goal of this paper is to summarize the botanical portion of the Biodiversity Project focusing on the most significant findings. The Hanford Site is a unique area from both a biogeographical and historical perspective. It supports unusual plant assemblages, many rare plant species, and a high degree of endemism, due to its underlying geology, landscape setting, topography, and climate. In addition, it is the largest area in the inland Northwest to be intentionally closed to grazing, agriculture, and residential development over a period during which human activity drastically altered much of the inland Northwest.

STUDY AREA

The Hanford Site is located within the Columbia Basin Ecoregion, an area that historically included over 6 million ha of steppe and shrub-steppe vegetation across most of central and southeastern Washington State, as well as portions of north-central Oregon (Franklin and Dyrness 1973). The Columbia Basin Ecoregion consists primarily of shrubs, perennial bunch-

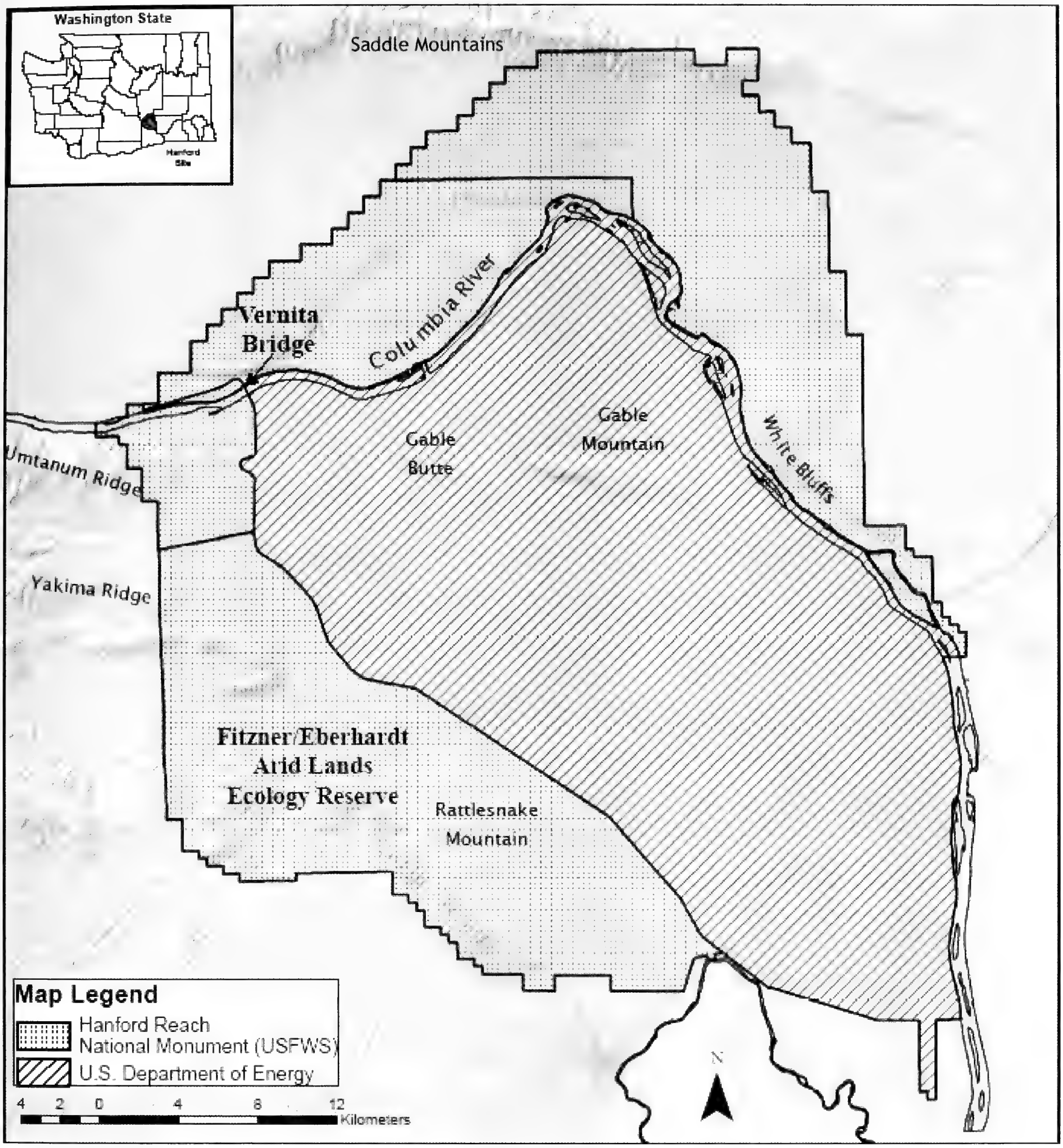

FIG. 1. Hanford Site (Benton, Grant, and Franklin counties, Washington): management areas and major topographic features.

grasses and a variety of forbs (Franklin and Dyrness 1973). It has undergone substantial loss and degradation in the post-European era due to intensive livestock grazing, introduction of invasive non-native plants, the advent of dryland wheat farming and irrigated agriculture, and altered fire regimes. Because the Hanford Site has been closed to all agricultural activities, including grazing, for nearly sixty years, its shrub-steppe plant ecosystem has been preserved in a condition and to an extent, that exists nowhere else (Soll et al. 1999). The Hanford Site supports many areas of high quality plant communities. The plant community portion of the Biodiversity Project identified 48 high quality occurrences of 17 terrestrial plant community types, and 6 high quality riparian wetland communities (Soll et al. 1999).

The Hanford Site is within the Central Basin climatological region, which is the hottest and driest climatological region in Washington. Average annual precipitation ranges from 35 cm at the summit of Rattlesnake Mountain to 16 cm near the Columbia River (Downs et al. 1993).

The Hanford Site is topographically variable (Fig. 1). Elevations within the Hanford Site range from 110 m along the Columbia River to 1100 m at the crest of Rattlesnake Mountain. Adjacent to the east side of the river are the steep bluffs of the Ringold Formation (the White Bluffs), which rise in places to over 185 m above the river. A number of long basalt anticlinal ridges traverse Hanford, including: Rattlesnake Mountain and the Rattlesnake Hills, Yakima Ridge, Umtanum Ridge, Saddle Mountains, and Gable Mountain. The only free-flowing section of the Columbia River in the U.S., known as the Hanford Reach, flows for 76 km from the northwest to the southeast through the northern portion of Hanford.

No perennial creeks drain to the Columbia River from the Hanford Site. Large dune fields occur on both sides of the Columbia River within the Hanford Site. The Hanford Site has a number of unique habitats and substrates, which include springs, sand dunes, vernal pools, riverine wetlands, caliche soils, basalt ridgetops, basalt-derived sand dunes, and alkaline areas.

Methods

The authors made over 15 visits to the Hanford Site between 1994 and 1997 to survey for vascular plant taxa considered rare in Washington at the time (Washington Natural Heritage Program 1994). We spent a total of 285 days in the field between late March and early September. We surveyed more than 19,000 ha. Field inventory methodology was based on habitat and flowering times of rare plant taxa potentially present in the area. The list of plants potentially present in the area was acquired from the Washington Natural Heritage Program, and the flowering times and habitat were obtained from the five-volume Vascular Plants of the Pacific Northwest (Hitchcock et al. 1955–1969). We focused inventories in areas with high quality vegetation associations, high diversity, and unusual substrates. Search intensity varied, depending on the quality of the habitat and the likelihood that the particular habitat could support rare plant populations. The lightest search intensity was a walked transect through the area, and the most intensive search intensity was a series of tightly spaced transects in which the entire area was visually examined, often several times during the growing season. A list of all plants was compiled, and specimens were deposited primarily at the University of Washington Herbarium (WTU). In some cases, taxonomic experts requested specimens, or isotypes were collected for other herbaria, and so specimens were also deposited at NY, US, WS, BRY, CAS, COLO, GH, K, MARY, MO, NY, RM, RSA, TEX, UC, and OSU. Nomenclature generally follows relevant Flora of North America treatments and the Integrated Taxonomic Information System (ITIS) database (Integrated Taxonomic Information System 2004). Existing specimens at the University of Washington Herbarium (WTU) and the Washington State Marion Ownbey Herbarium (WS) were used for comparison.

Results

We identified more than 400 species of vascular plants and numerous populations of 29 rare plants considered rare in Washington (Soll et al. 1999) during our three year inventory of the Hanford Site, of which three were previously undescribed, four were new records for the state, and one had long been ignored. These eight are the focus of this paper. The three previously undescribed entities are *Astragalus conjunctus* S. Watson var. *rickardii* S.L. Welsh, K.A. Beck and Caplow, *Eriogonum codium* Reveal, Caplow, and K.A. Beck, and *Physaria douglasii* (S. Watson) O'Kane and Al-Shehbaz subsp. *tuplashensis* (Rollins, K.A. Beck and Caplow) O'Kane and Al-Shehbaz. The three species new to Washington are *Cistanthe rosea* (S. Watson) Hershk., *Gilia leptomeria* A. Gray, *Loeflingia squarrosa* Nutt., and *Myosurus clavicaulis* M.E. Peck). The previously described species that had generally gone unnoticed by the American botanical community is *Festuca washingtonica* E.B. Alexeev). Each entity is discussed below, and the larger findings of the study are also summarized.

Previously Undescribed Entities

Astragalus conjunctus S. Watson var. *rickardii* S.L. Welsh, K.A. Beck & Caplow (Fabaceae)

The section *Conjuncti* Barneby in *Astragalus* L. is well represented in south-central Washington and north-central Oregon. *Astragalus conjunctus* S. Watson, *A. leibergii* M.E. Jones, *A. reventiformis* (Rydb.) Barneby, and *A. hoodianus* Howell all occur in this region (Barneby 1964). Although clearly belonging to the section *Conjuncti*, a number of *Astragalus* collections from Rattlesnake Mountain on the Hanford Site and from the nearby Horse Heaven Hills could not be satisfactorily assigned to any of the above species. We subsequently described a new variety, *A. conjunctus* var. *rickardii* (Welsh et al. 1997). In addition to Rattlesnake Mountain and Horse Heaven Hills, the variety is also known from northern Oregon.

The var. *rickardii* has erect, sessile, strigulose pods, campanulate to short-cylindric calyces, and a banner reflexed at about 45°. This combination of characteristics is not found in other members of the section (Welsh et al. 1997).

Astragalus conjunctus var. *rickardii* was found between 450 and 1070 m elevation in deep soil on

the upper portions of mostly north-facing slopes. It was primarily found in bunchgrass communities that are typically not currently grazed. Common associated species were *Artemisia tridentata* Nutt., *Pseudoroegneria spicata* (Pursh.) A. Löve, *Poa secunda* J. Presl., *Phlox longifolia* Nutt., *Balsamorhiza careyana* A. Gray, and *Crepis atribarba* A. Heller.

The variety is named in honor of Dr. William Rickard, a shrub-steppe ecologist and one of those responsible for the establishment of the Arid Lands Ecology Reserve. *Astragalus conjunctus* var. *rickardii* is currently included on the Watch list in Washington (Washington Natural Heritage Program 2005).

Eriogonum codium Reveal, Caplow & K.A. Beck (Polygonaceae)

During our 1995 botanical inventory of the Umtanum Ridge area of the Hanford Site we found a population of plants in the genus *Eriogonum* that did not resemble any known taxon. We subsequently published a new species, *Eriogonum codium* (Reveal et al. 1997). *Eriogonum codium*, or Umtanum desert buckwheat, is included in the subgenus *Eucycla* Nutt. The combination of cymose-umbellate inflorescences and sparsely tomentose flowers and achenes set *E. codium* apart from all other *Eucycla* taxa.

Eriognum codium forms low, shrubby mats up to 1 m in diameter, and bears yellow flowers in cymose-umbellate inflorescences atop short scapes. A single plant may have as many as 300 inflorescences. Inflorescences produce flowers from June through September. Our growth ring counts on several dead individual plants suggest potential life spans of greater than 100 years (Dunwiddie et al. 2001).

Eriogonum codium is known from one population that occurs in a discontinuous band 2.5 km long by 30 m wide. The population census in 1997 found 5200 adult plants in five small subpopulations on flat or gently sloping substrates above the steep north and northwest-facing slopes of Umtanum Ridge, at an elevation of approximately 375 m. A census of the population in 2005 found only 4418 adult plants in the population (a 15% decline in 8 years). The population was restricted to the exposed, barren basaltic flow top of the Lolo Flow, one of the many Columbia River basalt flows (Goff 1981). It was found with *Grayia spinosa* (Hook.) Moq., *Artemisia tridentata* Nutt., *Salvia dorrii* (Kellogg) Abrams, *Krascheninnikovia lanata* (Pursh) A.D.J. Meeuse & Smit, *Hesperostipa comata* (Trin. & Rupr.) Barkworth, *Poa secunda* J. Presl., *Pseudoroegneria spicata* (Pursh.) A. Löve, *Astragalus caricinus* (M.E. Jones) Barneby, *Bromus tectorum* L., *Mentzelia albicaulis* (Douglas ex Hook.) Douglas ex. Torr. & A. Gray, and *Cryptantha pterocarya* (Torr.) Greene.

In 1996, a wildfire killed 20% of the adult plants in the population. There were no signs of either fire tolerance or resprouting after the fire (Dunwiddie et al. 2001). A demographic monitoring study begun in 1997 has revealed aspects of the biology of this species that may affect its long-term viability. Despite abundant germination, only one *Eriogonum codium* seedling has survived to flowering since the commencement of studies in 1997. *Eriogonum codium* is considered Endangered in Washington (Washington Natural Heritage Program 2005), and a Candidate for federal listing under the Endangered Species Act (U.S. Fish and Wildlife Service 1999).

Physaria douglasii (S. Watson) O'Kane and Al-Shehbaz subsp. *tuplashensis* (Rollins, K.A. Beck and Caplow) O'Kane and Al-Shehbaz (Brassicaceae)

In 1883, T.S. Brandegee and F. Tweedie, who were employed as botanists for the Northern Transcontinental Survey (Rose 1904), collected a *Lesquerella* from the White Bluffs of the Columbia River. This fragmentary collection, dated July 1883, caused difficulties in a number of early treatments of *Lesquerella* (Gray and Watson 1895; Piper 1906), and was attributed to *L. douglasii* Wats. (Payson 1922; Rollins and Shaw 1973; Rollins 1993). *L. douglasii* is generally restricted to the valleys of the Kootenay and Columbia Rivers from northern Oregon to southern British Columbia (Rollins and Shaw 1973). In July of 1994, we collected flowering material from a *Lesquerella* on the White Bluffs that appeared to have both significant morphological and phenological differences from *L. douglasii*. These plants were subsequently described as a new species: *Lesquerella tuplashensis* (Rollins et al. 1996).

A recent treatment (Al Shehbaz and O'Kane 2002) has united *Lesquerella* with *Physaria* and united *L. douglasii* and *L. tuplashensis* under the single species name *Physaria douglasii* (S. Watson) O'Kane & Al-Shehbaz. *Lesquerella tuplashensis* was retained as a subspecies of *P. douglasii* and became *P. douglasii* subsp. *tuplashensis* (Rollins, K.A. Beck & Caplow) O'Kane & Al-Shehbaz, but not on the basis of new research or study of the two taxa. We are conducting morphometric and common garden experiments to further clarify the rank of this entity. At this time, ITIS still lists *Lesquerella tuplashensis* as the accepted name (ITIS 2005).

Physaria douglasii subsp. *tuplashensis* differs from *P. douglasii* subsp. *douglasii* in the following ways: the trichomes of the silique valves of *P. douglasii* subsp. *tuplashensis* are stipitate when viewed under a 10× lens, while those of *P. douglasii* subsp. *douglasii* are generally sessile and

appressed to the silique valve surface. The cauline leaves and the basal leaves of *P. douglasii* subsp. *tuplashensis* are broader and more imbricate than those of *P. douglasii* subsp. *douglasii* (Rollins et al. 1996). In addition, *P. douglasii* subsp. *tuplashensis* blooms in late May and early June and again in favorable years in late July and early August, while *P. douglasii* subsp. *douglasii* on riverine cobble on the Hanford Site blooms from late April to early May. We have never observed or collected *P. douglasii* subsp. *douglasii* in flower in late summer, nor have we seen any herbarium specimens of late summer flowering *P. douglasii* subsp. *douglasii*.

Physaria. douglasii subsp. *tuplashensis* was restricted to a narrow 17 km band on the upper portion of the White Bluffs of the Columbia River. The White Bluffs are composed of lacustrine sediments of the Ringold Formation (Newcomb 1958), capped by a cemented, highly alkaline (pH 8.4+) calcium carbonate paleosol (a "caliche" soil). Most of the population occurred on this caliche paleosol. Common associated plant species were *Grayia spinosa*, *Artemisia tridentata*, *Achnatherum contractum* (B.L. Johnson) Barkworth, *Bromus tectorum*, *Eriogonum microthecum* Nutt. var. *laxiflorum* Hook., and *Cryptantha spiculifera* (Piper) Payson.

Physaria douglasii subsp. *tuplashensis* is Threatened in Washington (Washington Natural Heritage Program 2005) and a Candidate for listing under the Endangered Species Act (U.S. Fish and Wildlife Service 1999). Both agencies list the entity as *Lesquerella tuplashensis*. "Tuplash" is the traditional Wanapum Indian name for the White Bluffs. The Wanapum tribe occupied the area of the White Bluffs until the first decades of the 20th century. They still actively work to protect the many native cultural sites on the Hanford Site.

Plants with Substantial Range Extensions

Cistanthe rosea (S. Watson) Hershkovitz (Portulacaceae)

Cistanthe rosea is a small annual previously known from central Oregon to central California east of the Sierra Nevada, east to Nevada, and in the Pacific Northwest in Butte County, Idaho (Hitchcock et al. 1955–1969). It generally occurs in sagebrush desert to arid montane forest. The Hanford Site population is the first report for this species in Washington. It represents a 340 km extension of its previous northern limit in Harney County, Oregon.

In 1997, we located a total of 12 small clusters of *Cistanthe rosea* north of Gable Mountain in the central portion of the Hanford Site, in an area approximately 1.5 × 1.2 kilometers. With an estimated total of 150 plants, the population was not large. The plants were growing in flat or gently sloping areas on dark basalt-derived sand substrate within low swales in relatively dense big sagebrush. *Cistanthe rosea* grew with *Artemisia tridentata*, *Bromus tectorum*, *Descurainea pinnata* (Walter) Britt., *Loeflingia squarrosa* Nutt., and *Mimulus suksdorfii* A. Gray. *Cistanthe rosea* is currently included on the Threatened list in Washington (Washington Natural Heritage Program 2005). It occured in an area that is not formally protected from Hanford activities.

Gilia leptomeria A. Gray (Polemoniaceae)

Gilia leptomeria is known from open, sandy or rocky areas in the Great Basin and Rocky Mountain states of the North American west (Kartesz 2003). In Washington, an accurate identification of *G. leptomeria* was difficult because Hitchcock and Cronquist (1973) did not recognize that there were two expressions within the concept of *G. leptomeria*. Day (1993) segregated *G. lottiae*, a more frequently encountered gilia of the sandy shrub-steppe in eastern Washington, from *G. leptomeria*, which is primarily known from southern Oregon south through California and east to Utah. The Jepson Manual (Hickman 1993) contains a key that differentiates *G. lottiae* from *G. leptomeria*. The Hanford Site populations are the first reported for *G. leptomeria* in Washington, and our collections were confirmed by Alva Day. It represents a 340 km extension of its previous northern limit in Malheur County, Oregon.

We found *Gilia leptomeria* in a number of localities on the Hanford site, including the White Bluffs, Umtanum Ridge, north of Gable Mountain, and the gravelly bluffs north of the Columbia River in the vicinity of Vernita Bridge. The Hanford Site populations were small, at least in the years we saw them. When we surveyed them in 1995 and 1997, most of the eight populations located had 100 plants or less, for an estimated total of less than 1000 plants. We observed *G. leptomeria* growing in a variety of habitats and substrates, including basalt dunes, caliche soil, gravelly slopes, and shrub-steppe. Commonly observed associates of *G. leptomeria* included *Artemisia tridentata*, *Poa secunda*, *Bromus. tectorum* L., *Astragalus caricinus*, *Salvia dorrii*, and a number of other annual species. It was found growing with several other plants considered rare in Washington. Currently, *G. leptomeria* is included on the Threatened list for Washington (Washington Natural Heritage Program 2005). Some of the populations occurred in areas that are not formally protected from Hanford activities.

Loeflingia squarrosa Nutt. (Caryophyllaceae)

This is the first report of *Loeflingia squarrosa* for Washington. It is generally found at less than

1200 m in California and northern Baja California, and from southeastern Oregon (Hickman 1993). Our collections represent a 420 km extension of its previous northern limit near Malheur Lake and Frenchglen in Harney County, Oregon (Peck 1961).

We found *Loeflingia squarrosa* in a number of localities on the Hanford site. The eight Hanford Site populations were relatively large in the years we saw them. When we surveyed them in 1995 and 1997, we estimated a total of at least 8000 plants. At Hanford, *L. squarrosa* typically grew in flat or gently sloping areas on dark basalt derived sand substrate within low swales in relatively dense big sagebrush. One population was growing in a vernal pool on Umtanum Ridge. Commonly observed associates of *L. squarrosa* included *Artemisia tridentata*, *Poa secunda*, *Bromus tectorum*, *Cryptantha circumscissa* (Hook. & Arn.) I.M. Johnst., *Mimulus suksdorfii*, and a variety of other annual species. Currently, *L. squarrosa* is included on the Threatened list for Washington (Washington Natural Heritage Program 2005). Most populations of *L. squarrosa* occurred in areas that are not formally protected from Hanford activities.

Myosurus clavicaulis Peck (Ranunculaceae)

In 1997, we found a population of unusual *Myosurus* plants in a vernal pool on the east end of Umtanum Ridge on the Hanford Site. Plants from this site resemble *Myosurus* plants of certain vernal pool populations in coastal southern California, northern Baja California, and Harney County, Oregon. Plants from these populations share most of the morphological characteristics of *Myosurus minimus* L., but have short, curved scapes, so that the heads of the achenes are immersed in the leaves (Whittemore 1997). Since 1997, *M. clavicaulis* has been found at several additional vernal pool sites in eastern Washington by other workers (Washington Natural Heritage Program database).

Stone (1959) suggested that this form of *Myosurus* resulted from past hybridization between the two species *Myosurus minimus* L. and *M. sessilis* S. Watson. during a time when *M. sessilis* had a wider range than it does now. Currently, *M. sessilis* is not known to occur north of Umatilla Co., Oregon (Hitchcock and Cronquist 1973; Whittemore 1997). At the coastal southern California, northern Baja California, Oregon, and Washington sites, this expression occurs as a self-sustaining entity, independent of *M. sessilis* and often independent of *M. minimus*. The taxonomic status of these plants is obscured by the presence of morphologically identical plants in the Central Valley of California. The Central Valley plants are non-persistent products of on-going hybridization between *M. minimus* and *M. sessilis* (Whittemore 1997). When he examined the Hanford Site collections in 1997, Whittemore suggested that we call them *Myosurus clavicaulis* Peck to distinguish them from typical *M. minimus* and plants from *M. minimus* × *sessilis* hybrid swarms.

The Washington populations represent a more than 375 km extension of its previous northern limit in Harney County, OR. When surveyed in 1997, there were estimated to be over 1000 plants in the Hanford Site population. The population was found on the south and southeast-facing sides of the farthest west vernal pool (20 × 20 m) in a set of vernal pools on Umtanum Ridge. Plants grew on the drying edges of the pool, with *Veronica peregrina* L. ssp. *xalapensis* (Kunth) Pennell, *Camissonia andina* (Nutt.) Raven, *Myosurus apetalus* Gay, *Epilobium minutum* Lindl. ex Lehm., *Artemisia rigida* (Nutt.) A. Gray, mosses and lichens. *Myosurus clavicaulis* on the Hanford Site is self-sustaining and does not occur within close proximity of either *M. sessilis* or *M. minimus*. Currently, *M. clavicaulis* is included on the Sensitive list for Washington (Washington Natural Heritage Program 2005).

Previously Unrecognized Species

Festuca washingtonica Alexeev

In 1995, we collected an unusual *Festuca* high on the north-facing slopes of Rattlesnake Mountain in the Arid Lands Ecology Reserve (ALE). We sent this collection to B. Wilson at Oregon State University, who identified it as *Festuca washingtonica* Alexeev. The history of this taxon is as follows: in 1960, J. G. Smith collected what he called *F. rubra* L. in Peavine Canyon, Chelan County, Washington. A portion of the collection was eventually sent to Leningrad. From that lone specimen, E.B. Alexeev (1982) described *F. washingtonica*, with the note (translated from Russian) "in habit and anatomical structure of the leaf blades this species resembles *F. rubra*. However, within the limits of the very polymorphic latter species, we do not know of a single taxon with leaf blades that are externally scabrous as in *F. washingtonica*." (Alexeev 1982). Alexeev's new fescue species was largely ignored until our collections of it in 1995. Based on our collections from the Hanford Site and from other locations, B. Wilson wrote an expanded description of *F. washingtonica*, (Wilson 1999).

Festuca washingtonica is a relatively large, bright to deep green, cespitose fescue with flat leaves 1 to 6 mm wide, lemmas scabrous or pubescent, and ovary apex typically pubescent. According to Wilson (1999), "*Festuca washingtonica* differs from *F. viridula* in having closed sheaths, extravaginal shoots, and abaxial to adaxial sclerenchyma strands in the leaves, illustrated by Alexeev (1982)". *Festuca washing-*

tonica may belong in the subgenus *Festuca*, although analysis of seed proteins suggests problems with that classification (Aiken et al. 1998).

Festuca washingtonica appears to be endemic to seasonally moist habitats in deep soil of lightly grazed or ungrazed shrub-steppe communities east of the Cascade Range in Washington, including the ALE Reserve on the Hanford Site. On the ALE Reserve, plants occurred just below the top of Rattlesnake Mountain in rocky silt loam at an elevation of 1100 m. This was within an *Artemisia tripartita*/*Festuca idahoensis* plant association with *Lupinus arbustus* Douglas ex Lindl. ssp. *calcaratus* (Kellogg) D. Dunn, *Melica bulbosa* Geyer, *Poa cusickii* Vasey, *P. secunda* J. Presl., and *Senecio integerrimus* Nutt.

Since 1995, *Festuca washingtonica* has been collected from other counties in eastern Washington, including Yakima, Kittitas, Chelan and Okanogan Counties, suggesting that the taxon may have been overlooked and/or mis-identified by past researchers. Most sites where it grows are protected from livestock, either administratively or topographically. To our knowledge, it has not been collected outside of Washington.

Other Findings

The Hanford Site supports approximately 725 different kinds of vascular plants (Sackschewsky and Downs 2001). Of these, 29 (4%) are listed by the state of Washington as rare (Washington Natural Heritage Program 2005). During our three-year botanical inventory of the Hanford Site, we identified more than 500 species of plants and 112 populations of 26 state-listed rare plants (Soll et al. 1999). Two of these rare plants are endemic to the Hanford Site: *Physaria douglasii* subsp. *tuplashensis* and *Eriogonum codium*. Four are narrow regional endemics that also occur outside the boundaries of the Hanford Site: *Astragalus columbianus* Barneby, *A. conjunctus* var. *rickardii*, *Lomatium tuberosum* Hoover, and *Penstemon eriantherus* Pursh var. *whitedii* (Piper) A.Nelson. Four are more widespread regional endemics that are also known from elsewhere in the Columbia Basin: *Camissonia pygmaea* (Douglas ex Lehm.) Raven, *Cryptantha leucophaea* (Douglas ex Lehm.) Payson, *Erigeron piperianus* Cronquist, and *Rorippa columbiae* (Suksd. ex B.L.Rob.) Suksd. ex Howell. There are also a number of regional endemics known from the Hanford Site that are not considered rare in Washington.

Eighteen species found by the authors on the Hanford Site are widely distributed in North America but are disjunct or peripheral in Washington. These are considered rare and are tracked by the Washington Natural Heritage Program: *Ammannia robusta* Heer & Regel, *Anagallis minima* (L.) Krause, *Astragalus geyeri* A. Gray, *Camissonia minor* (A. Nelson) Raven, *Castilleja minor* (a. Gray) Gray ssp. *minor*, *C. spiculifera* (Piper) Payson, *Cistanthe rosea*, *Cryptantha scoparia* A. Nelson, *Cuscuta denticulata* Engelm. var. *denticulata*, *Cyperus bipartitus* Torr., *Eatonella nivea* (D.C. Eaton) A. Gray, *Gilia leptomeria*, *Hypericum majus* (Gray) Britt., *Lipocarpha aristulata* (Covill) G.C. Tucker, *Loeflingia squarrosa*, *Mimulus suksdorfii* Gray, *Myosurus clavicaulis* Peck, *Oenothera caespitosa* Nutt., and *Rotala ramosior* (L.) Koehne. *Festuca washingtonica* is abundant enough state-wide that it is not tracked by the Washington Natural Heritage Program.

Discussion and Conclusion

The findings of the botanical portion of the Hanford Biodiversity Project have reinforced the importance of the Hanford Site for conservation of shrub-steppe vascular plants. The very high plant species richness of the Hanford Site is likely the result of a combination of geographic and historical factors. The Columbia River corridor, which bisects the Hanford Site, is known to support a large number of regional and narrow endemics (Hitchcock and Cronquist 1973). The Hanford Reach, the only undammed portion of the Columbia River, supports emergent wetland communities that include populations of several rare species that were once widely collected but are now uncommon elsewhere on the river (Soll et al. 1999). In addition, the unique climate of the Hanford Site supports a number of species that are more common in desert areas of the Great Basin to the south and east (Kartesz 2003). The diversity of unique substrates and habitats on the Site provide habitat for a large number of state-listed rare plants and endemics, including those reported above.

Much of the biodiversity of the Hanford Site might have been lost without its unique history. If the Hanford Site had not been acquired by the U.S. Government in 1943, it would most certainly resemble the rest of the lower Columbia Basin where population growth, large-scale irrigation projects, livestock grazing, and noxious weeds have significantly reduced and/or degraded available habitat for many plants. The relatively large Hanford Site, taken with the similar sized Department of Defense Yakima Training Center to the west, constitute the largest remaining blocks of relatively undisturbed shrub-steppe in the Columbia Basin Ecoregion (Soll et al. 1999).

Of the state-listed rare plants found on the Hanford Site, 18 (62%) are annuals, and 3 of these have not been found elsewhere in Washington. Because of the relatively high number of rare annuals on the Hanford Site, it is an important location for the conservation of rare annuals in Washington. Annuals tend to occur in

TABLE 1. SUMMARY OF ADDITIONS TO THE VASCULAR FLORA OF WASHINGTON FROM THE HANFORD BIODIVERSITY PROJECT.

Species	Previously known range	Washington counties where currently known	Washington Natural Heritage Program status (2005)
Astragalus conjunctus var. *rickardii*	Not known	Benton	Watch
Cistanthe rosea	Oregon, California, Idaho, Nevada, Wyoming	Benton	Threatened
Eriogonum codium	Not known	Benton	Endangered
Festuca washingonica	Chelan County, Washington	Benton, Yakima, Kittitas, Chelan, Okanogan	None
Gilia leptomeria	California, Oregon, Idaho, Colorado, New Mexico, Arizona, Nevada, Wyoming, Montana	Franklin, Grant, Benton	Threatened
Physaria douglasii subsp. *tuplashensis*	Not known	Franklin	Threatened
Loeflingia squarrosa ssp. *squarrosa*	Western states not including Pacific NW	Benton	Threatened
Myosurus clavicaulis	California, Oregon	Adams, Spokane, Benton	Sensitive

moist microhabitats in open sandy or gravelly soils, and many of these sites elsewhere in the state have been disturbed and compacted by grazing and invaded by *Bromus tectorum*.

At the time that the Hanford Biodiversity Study began, the conservation of the biodiversity of the Hanford Site was not assured. There was a powerful local movement to distribute most of the land north of the Columbia River to private landowners for agricultural development. The future protection of the ALE Reserve was also in question. Since that time, the Hanford Reach has been declared a Wild and Scenic River and much of the Hanford Site, including the ALE Reserve, has been set aside as the Hanford Reach National Monument. However, the central portion of the Site, which supports a number of rare plant populations, is still primarily dedicated to nuclear waste storage and clean-up. The *Eriogonum codium* population, although formally within the Hanford National Monument, is not in an area currently managed by the USFWS.

Even with protection, active, on-going management will be necessary to maintain the biodiversity of the Hanford Site. In particular, noxious weeds (e.g., *Bromus tectorum* L., *Salsola kali* L., *Centaurea solstitialis* L. and others) and wildfire will bring adverse changes to natural vegetation communities over time. Nonetheless, the future of the vascular plant diversity of the Hanford Site appears considerably better than it did in 1994, when the Hanford Biodiversity Project was initiated.

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APPENDIX 1

RELEVANT HERBARIUM COLLECTIONS BY THE AUTHORS OF RARE PLANTS ON THE HANFORD SITE

Astragalus conjunctus var. *rickardii* Welsh, K.A. Beck & Caplow (FABACEAE). TYPE: U.S.A., Washington, Benton Co. Hanford Site, on northeast-facing slopes of Rattlesnake Mountain, with *Artemisia tridentata*, *Poa sandbergii*, 1036 meters, T11N R26E sect. 30 NW¼ of SW¼, 29 May 1995, *Kathryn Beck & Florence Caplow 95-083*, (Holotype: BRY!; Isotypes: NY!, US!, WTU!, WS!); Benton County, Horse Heaven Hills, Chandler Butte, BLM owned, in silt loam, upper north-facing slopes, with *Agropyron spicatum*, *Poa cusickii*, *Artemisia tridentata*, *Poa sandbergii*, 600 meters, T9N R26E sect. 22 SE¼ of NW¼, 14 April 1995, *Florence E. Caplow & Kathryn A. Beck 95-022* (BRY, WTU).

Cistanthe rosea S. Watson (PORTULACACEAE). Benton Co., Hanford Site north of Gable Mountain in basalt derived sands, in a small swale, with *Artemisia tridentata*, *Bromus tectorum*, *Descurainea pinnata*, *Loeflingia squarrosa* ssp. *squarrosa* and *Mimulus suksdorfii*, 1–2% slope, south exposure, 150 meters, T13N R26E sect. 2 SE¼ of S¼, 28 May 1995, *Florence E. Caplow & Kathryn A. Beck 95-078* (WTU).

Eriogonum codium Reveal, Caplow & K.A. Beck (POLYGONACEAE). TYPE: U.S.A., Benton Co., Hanford Site, on the northern edge of Umtanum Ridge west of Washington Highway 24 overlooking the Columbia River about 38 air miles northwest of Richland, on volcanic soil, with *Grayia spinosa*, *Artemisia tridentata*, *Salvia dorrii*, *Hesperostipa comata*, and *Pseudoroegneria spicata*, 350 meters, T13N R24E sect. 13, 27 June 1995, *Reveal, Caplow and Sackschewsky 7484* (Holotype: US; Isotypes: BM, BRY, CAS, COLO, GH, K, MARY, MO, NY, RM, RSA, TEX, UC, WS, WTU and elsewhere); Also in reddish to black, hard-packed basalt gravel, with *Artemisia tridentata*, *Salvia dorrii*, *Poa sandbergii*, *Bromus tectorum*, *Phacelia linearis*, 300°, 3% slope, T13N R24E sect. 13 NE¼ of SW¼, 31 May 1995, *Florence E. Caplow & Kathryn A. Beck 95-084* (WTU, WS).

Festuca washingtonica E.B.Alexeev (POACEAE). Benton Co., Arid Lands Ecology Reserve, Hanford Site, Rattlesnake Mountain, in a narrow strip just below the top of the mountain, in the "snowmelt" zone, in rocky silt loam, with *Artemisia tridentata*, *Lupinus laxiflorus* var. *calcaratus*, *Poa nevadensis*, *Senecio integerrimus*, *Festuca idahoensis*, *Melica bulbosa*, and *Poa cusickii*, 45°, 35%, 1130 meters, T11N R26E sect. 30 NW¼ of SW¼, 4 June 1995, *Florence E. Caplow & Kathryn A. Beck 95088* (OSU, WTU); Chelan Co., Wenatchee National Forest, Wenatchee Mountains, on lower west-facing dry slopes of a small tributary in Peavine Canyon, with *Pinus ponderosa*, *Symphoricarpos albus*, *Salix* sp., *Acer douglasii*, *Prunus emarginata*, *Purshia tridentata*, *Lupinus leucophyllus*, *Aster foliaceus*, *Agropyron spicatum*, and *Poa pratensis*, 270°, 5%, 630 meters, T22N R19E sect. 15 SW¼ of SE¼, *Kathryn A. Beck & Florence E. Caplow 96-052* (OSU, WTU).

Gilia leptomeria A. Gray (POLEMONIACEAE). Grant Co., Hanford Site, Saddle Mountain NWR, on upper slopes of gravelly bluff north of Vernita Bridge on the Columbia River, with *Salvia dorrii*, *Camissonia pygmaea*, and *Eatonella nivea*, south exposure, 30%, 215 meters, T14N R25E sect. 31 SE¼, 15 May 1995, *Florence E. Caplow & Kathryn A. Beck 95-035* (WTU); Franklin Co., Hanford Site, Wahluke Wildlife Area, White Bluffs of the Columbia River, near top of bluffs, in caliche soil, with *Eriogonum microthecum*, *Poa secunda*, *Bromus tectorum*, *Astragalus caricinus*, and *Eurotia lanata*, western exposure, 285 meters, T13N R27E sect. 25, 19 May 1995, *Florence E. Caplow & Kathryn A. Beck 95-055* (WTU); Also on sparsely vegetated ground in sand and caliche, with *Chrysothamnus nauseosus*, *Bromus tectorum*, *Astragalus caricinus*, *Artemisia tridentata*, *Astragalus succumbens*, and *Gilia sinuata*, 220°. 5%, T13N R28E sect. 19 SE¼ of NW¼, 31 May 1997, *Florence E. Caplow & Kathryn A. Beck 97-042* (WTU); Benton Co., Hanford Site Umtanum Ridge, ridge-top, at edges of steep north-facing slopes, in fine reddish to blackish basalt, gravel and pumice, with *Artemisia tridentata*, *Eriogonum codium*, *Bromus tectorum*, *Poa secunda*, and *Salvia dorrii*, 350 meters, T13N R24E sect. 13 NE¼ of SW¼, 31 May 1995, *Florence E. Caplow & Kathryn A. Beck 95-076* (WTU); Additional unvouchered populations were located. Plants were determined by Alva Day, 1995.

Physaria douglasii subsp. *tuplashensis* Rollins, K.A. Beck & Caplow (BRASSICACEAE). TYPE: U.S.A. Washington, Franklin County: White Bluffs, above the Columbia River, caliche soil at edge of eroding bluff, with *Artemisia tridentata*, *Astragalus caricinus*, *Cryptantha spiculifera*, *Eriogonum microthecum*, and *Poa sandbergii*, T13N R27E sect. 11 W1/2, 20 July 1994, *Kathryn A. Beck & Florence Caplow 94-001* (Holotype: GH; Isotype: WTU). Franklin Co., Hanford Site, Wahluke Wildlife Area, White Bluffs northeast of the Columbia River, near powerlines, on the leading edge of the bluffs, in hard caliche soils, with *Poa secunda*, *Astragalus caricinus*, *Cryptantha spiculifera*, *Eriogonum microthecum* var. *laxiflorum*, 300 meters, T13N R27 E sect. 24 NE¼ of NE¼, 19 May 1995, *Florence E. Caplow & Kathryn A. Beck 95-053* (WTU, GH). Upper slopes near mouth of Ringold Canyon, in loose caliche soils, with *Poa secunda*, *Bromus tectorum*, *Amsinckia tessellata*, 220 meters, T12N R28E sect. 11 NW¼ of SW¼, 1 June 1995, *Florence E. Caplow & Kathryn A. Beck 95-086* (GH).

Loeflingia squarrosa Nutt. ssp. *squarrosa* (CARYOPHYLLACEAE). Benton Co., Hanford Site, north of Gable Mountain in basalt-derived, stabilized sand dunes, on a sandy berm of a little-used road, with *Artemisia tridentata*, *Poa secunda*, *Bromus tectorum*, *Cryptantha circumcissa*, and *Mimulus suksdorfii*, 145 meters, T13N R26E sect. 13, 16 May 1995, *Florence E. Caplow & Kathryn A. Beck 95-039* (WTU); Benton Co., Hanford Site, between two main portions of Gable Butte, in shrub-steppe at edges of vernal pool in rocky basalt layer, with *Artemisia tridentata*, *Gnaphalium palustre*, *Camissonia andina*, *Juncus bufonius*, *Epilobium minutum*, moss spp., and lichen spp., 175 meters, T13N R26E sect. 18 SW¼ of SW¼, 20 May 1997, *Florence E. Caplow & Kathryn A. Beck 97-023* (WTU); also south of Gable Mountain, plants growing in shrub-steppe, in barren basalt-derived sand, along a little-used sandy road, with *Artemisia tridentata*, *Ambrosia acanthicarpa*, *Pectocarya linearis*, *Bromus tectorum*, and *Mimulus suksdorfii*, 160 meters, T13N R26E sect. 25 SE¼ of NE¼, 29 May 1997, *Florence Caplow & Kathryn A. Beck 97-041* (WTU). Plants were verified by Ronald Hartman, 1995. Additional unvouchered populations were located, including ones at the eastern end of Umtanum Ridge, in a vernal pool and also in a swale amidst shrub-steppe.

Myosurus clavicaulis Peck (RANUNCULACEAE). Benton Co., Hanford Site, top of east end of Umtanum Ridge, plants growing on dried edges of vernal pool in depression of basalt layer, with *Veronica peregrina* var. *xalapensis*, *Camissonia andina*, *Myosurus apetalus*, *Epilobium minutum*, *Artemisia rigida*, moss spp., and lichen spp., 315°, 1% slope, 195 meters, T13N R25E sect. 17 ¼ of ¼, 6 May 1997, *Florence E. Caplow & Kathryn A. Beck 97-010* (US, WTU); same location, 7 May 1997, *Florence E. Caplow & Kathryn A. Beck 97-014* (WTU), verified by Alan Whittemore.

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A RECONSIDERATION OF *BRODIAEA MINOR* (BENTH.) S. WATSON AND *BRODIAEA PURDYI* EASTWOOD (THEMIDACEAE), WITH THE RESURRECTION OF *BRODIAEA NANA* HOOVER

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ABSTRACT

A review of taxonomic literature, examination of existing herbarium specimens, and a morphological study of field-collected material demonstrates that species circumscriptions have been misapplied for the small-flowered *Brodiaea* species with spreading perianth lobes and floral tubes narrowed above the ovary. The results of these studies demonstrate that Niehaus's (1971) concept of *B. purdyi*, polyploid plants that occur in woodland habitats in the northern Sierra Nevada foothills, applies to the taxon originally described as *B. minor*, placing *B. purdyi* in synonymy with *B. minor*. Niehaus's concept of *B. minor*, diploid plants occurring in vernal pool terrain, applies only to those populations originally described as *Brodiaea nana*, which is resurrected at species rank.

Key Words: Themidaceae, *Brodiaea*, taxonomic revision, California.

The genus *Brodiaea* (Themidaceae) consists of approximately 14 or 15 species, almost entirely restricted to the California Floristic Province (Niehaus 1971, 1980; Keator 1993; Pires 2002). *Brodiaea* has a rich taxonomic history and has been placed variously in Liliaceae, Amaryllidaceae, and Alliaceae (Hoover 1939; Keator 1967, 1989; Niehaus 1971, 1980). Recent phylogenetic studies, however, place *Brodiaea* and relatives not with *Allium* but with Hyacinthaceae and other families (Fay and Chase 1996; Fay et al. 2000; Pires et al. 2001; Pires and Sytsma 2002). As a result, *Brodiaea* has been reassigned to the family Themidaceae or a more inclusive Asparagaceae (Angiosperm Phylogeny Group 2003).

These studies have focused on relationships among families and genera and have not addressed relationships within *Brodiaea*, which remain poorly resolved despite having been monographed twice (Hoover 1939; Niehaus 1971). Species circumscriptions and relationships among species historically have been difficult to elucidate, largely because study of fresh material is crucial for comparison of the diagnostic floral features, which are obliterated when specimens are pressed and dried (Greene 1886; Hoover 1939). Pires (2002) points out the need to prepare open flowers when making herbarium specimens, but even with fresh material, making a determination with confidence can often be frustrating.

The small-statured species with spreading perianth lobes and floral tubes that are narrowed above the ovary exemplify this taxonomic difficulty. Current floristic treatments of *Brodiaea* (Keator 1993; Pires 2002) recognize two species, *Brodiaea minor* (Benth.) S. Watson and *Brodiaea purdyi* Eastwood, based on Niehaus's (1971) monograph of the genus. Niehaus differentiated between the two species based on morphology, cytology, and ecology. However, it is often not possible to assign specimens unambiguously to one or the other species, using the current taxonomic keys (Oswald 1994; personal observation).

In this paper, I show that the frustration with species determinations using current floristic treatments is not due simply to an inadequate diagnostic key, but stems from a more fundamental error. I provide a morphometric analysis supporting Niehaus's recognition of two taxa at species rank, but I demonstrate that Niehaus misapplied the name *B. minor* and did not correctly circumscribe all populations under the correct species concepts. I discuss the source of Niehaus's error and clarify the nomenclature. In addition, I discuss the relationship of these two species with other members of the genus.

METHODS

I examined herbarium specimens of *B. minor* and *B. purdyi*, as circumscribed by Niehaus (1971), in the principal collections of both species (herbaria consulted: JEPS, UC, CHSC, DAV) and photographs of the types of *B. minor, B. purdyi*, and *B. nana*. I sampled 36 populations throughout the ranges, based on localities provided on the specimen labels. I collected fresh material and dissected one flower from 10 plants in each population, using flowers at approximately the same stage of anthesis, to minimize variation due to any change in flower size from the beginning to the end of anthesis. I measured 11 floral characters and noted the shape and position of the floral parts. I employed principal components analysis, using the SYSTAT 11

statistics package (SYSTAT Software, Richmond, CA), to reduce the number of variables and simplify the morphological comparison. The analysis was performed using the mean floral measurements from each population. Factor scores for the first two principal components were then plotted to determine whether discrete groups of populations could be recognized.

Results and Discussion

Taxonomic Review

Theodor Hartweg collected the type of *Brodiaea minor*. In the spring of 1847, he had traveled to California on a mission to collect botanical specimens for the Horticultural Society of London (Hartweg 1848). Hartweg made numerous collections during his stay at the ranch of "Mr. L.", in the northern Sacramento Valley (undoubtedly Peter Lassen, who homesteaded in southern Tehama County, near the present town of Vina (Swartzlow 1964)). During a visit to the foothills east of the ranch, he collected specimens that later became the type of *Brodiaea grandiflora* Sm. var. *minor* Benth. Sereno Watson (1879) later raised var. *minor* to species rank.

Greene (1894) apparently initiated some confusion by applying the name *B. minor* to all of the small-flowered brodiaeas in the Central Valley and adjacent Sierra Nevada foothills. Subsequently, Alice Eastwood (1896) described a "new" species from the northern Sierra Nevada foothills, *Brodiaea purdyi*, noting the long, narrow perianth lobes as the distinguishing feature of this species. Jepson (1922) recognized that Greene had encompassed several different taxa under the name *B. minor* and that *B. purdyi* was synonymous with *B. minor*, as originally described by Bentham. Jepson applied the name *Brodiaea synandra* (Heller) Jepson to the small-flowered plants of the Central Valley that, like *B. minor*, had the perianth tube narrowed above the ovary. Unfortunately, Jepson did not have access to the type specimen of *B. synandra*, which actually is conspecific with the earlier-published *Brodiaea leptandra* (E. Greene) Baker. Jepson also repeated Greene's error, citing specimens now assigned to several different species, including *B. coronaria* and *B. terrestris*, within his circumscription of *B. synandra*.

Hoover (1936, 1939) eventually sorted out the nomenclatural confusion. Hoover (1939) was the first to monograph the genus and developed most of the species concepts that are still used to circumscribe the taxa. *Brodiaea* species have traditionally been differentiated on the basis of the shape and position of the floral parts, and Hoover followed this tradition by recognizing species when there were discrete differences in morphology and recognizing varieties when taxa differed primarily in the size of the floral parts. For the small-flowered plants along the east side of the Central Valley, he proposed the name *Brodiaea nana*, because of their small stature, having scapes less than 5 cm tall. Hoover (1939) subsequently reduced *B. nana* to a variety of *B. minor*, citing his observations that the two taxa intergraded morphologically.

Niehaus (1971) expanded on Hoover's work with *Brodiaea* by incorporating observations from anatomy, cytology, palynology, flavonoid chemistry, ecology, and hybridization studies. Although his study tended to support Hoover's taxonomic framework, he expanded some of the morphologically-based species concepts in *Brodiaea* to include data from cytology and ecology. Niehaus recognized two small-statured, small-flowered species with spreading perianth lobes and floral tubes that are narrowed above the ovary, one consisting of populations of diploid ($n = 6$) plants growing in vernal pool terrain along the eastern edge of the Central Valley, the other consisting of tetraploid ($n = 12$) and octaploid ($n = 24$) populations occurring in foothill habitats, often on gabbro or serpentine. To the former species, which essentially followed Hoover's concept of *B. nana*, he applied the name *B. minor*, placing *B. nana* in synonymy. He resurrected the name *B. purdyi* to apply to the latter species. Recent floristic treatments of *Brodiaea* (Keator 1993; Pires 2002) mostly followed Niehaus's treatment of the genus and maintained both *B. minor* and *B. purdyi* at species rank, although Keator noted that *B. purdyi* might merit placement as a subspecies of *B. minor*.

Morphological Study

The morphological study found that plants from the 36 sampled populations could be unambiguously assigned to one of two groups, but not to the groups represented by *B. minor* and *B. purdyi* as circumscribed by Niehaus (1971). First, two groups were differentiated by the shape and position of the stamens and staminodes. The first group of populations (Group A) had stamen morphology that was unusual for the genus and most similar to that described for *B. pallida* (Hoover 1938), including the presence of prominent papillae on the abaxial surface of the anthers (Fig. 1a). The connective broadened towards the apex, which was widely V-notched (Fig. 1a, b), and the filaments were short and abaxially winged (V- or Y-shaped in cross-section [Fig. 1c]). The staminodes were short, broad, and erect, with slightly inrolled margins (Fig. 1d, 2a). The styles were about 1.5 times longer than the ovary (Fig. 1e).

Stamen morphology in the second group of populations (Group B) was not remarkably different from that in many other *Brodiaea*

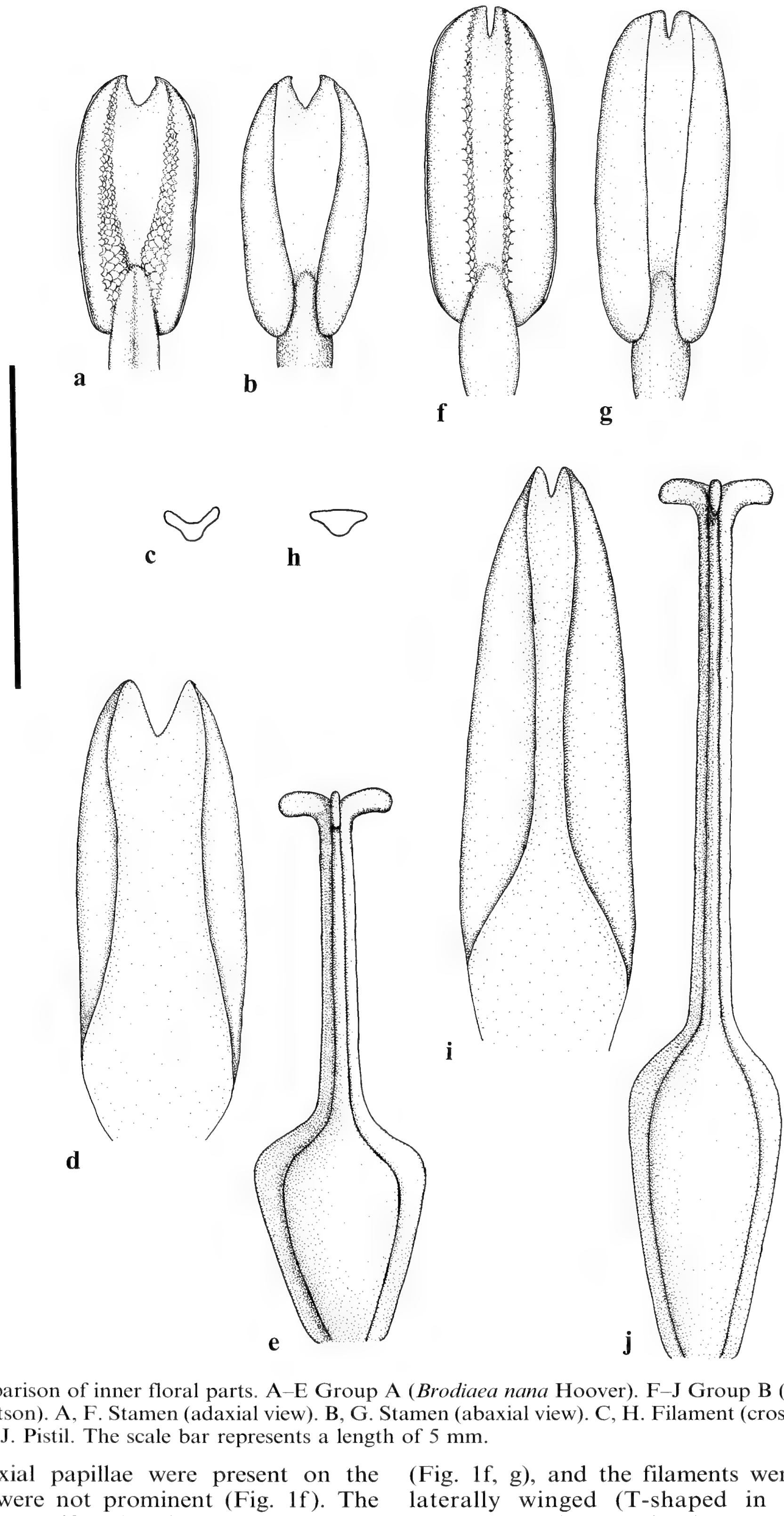

FIG. 1. Comparison of inner floral parts. A–E Group A (*Brodiaea nana* Hoover). F–J Group B (*Brodiaea minor* (Benth.) S. Watson). A, F. Stamen (adaxial view). B, G. Stamen (abaxial view). C, H. Filament (cross-section). D, I. Staminode. E, J. Pistil. The scale bar represents a length of 5 mm.

species. Abaxial papillae were present on the anthers but were not prominent (Fig. 1f). The connective was uniformly wide to only slightly broader at the apex, which was narrowly notched (Fig. 1f, g), and the filaments were longer and laterally winged (T-shaped in cross-section [Fig. 1h]). The staminodes were longer and narrower with strongly inrolled margins (Fig. 1i)

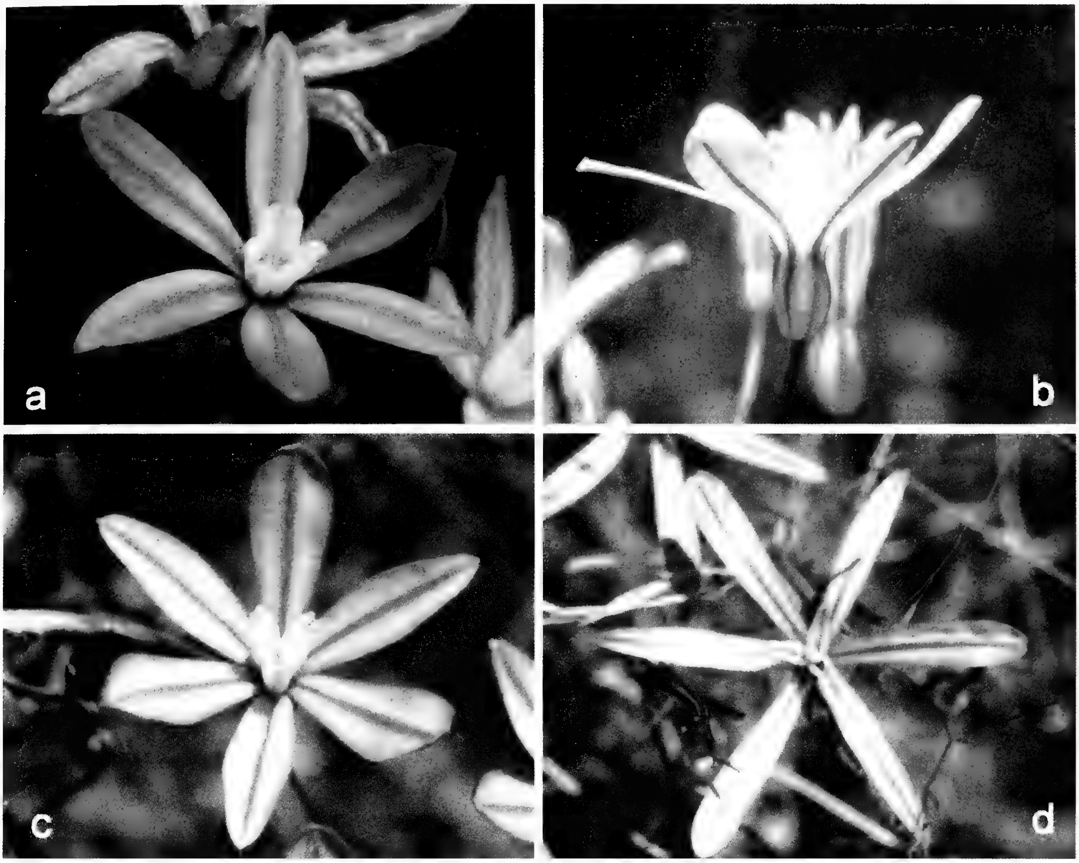

FIG. 2. Comparison of flowers. A, B *Brodiaea nana* Hoover. A. Top view. B. Lateral view, showing constriction above the ovary. C, D *Brodiaea minor* (Benth.) S. Watson. C. Typical form. D. Narrow-lobed form described as *B. purdyi* Eastw.

and were erect to recurved at the tip (Fig. 2c, d). The styles were about 1.75 times the length of the ovary (Fig. 1j).

The principal components analysis reduced the floral variables to two factors (Table 1). The first principal component, which explained almost 79% of the variation, appeared to be a size factor, primarily loading on length of the floral parts. The second principal component also appeared to be a size factor, but loading on the size of the perianth lobes (length and width). The plot of the two principal components also separated the populations into two groups that corresponded precisely with Groups A and B, but not to *B. minor* and *B. purdyi* as currently circumscribed (Fig. 3).

Group A corresponds closely to Hoover's (1936) original circumscription of *Brodiaea nana* and includes populations along the eastern edge of the Central Valley, ranging from Butte County to Merced County, where the type was collected. Group A includes all of the populations Niehaus (1971) determined to be diploid. Group B consists of populations Niehaus assigned to *B. purdyi* but also includes populations he assigned to *B. minor*. Populations comprising Group B range from the Sierra Nevada foothills to the northern Sacramento Valley in Butte and Tehama Counties, encompassing the type localities of both *B. minor* and *B. purdyi*. Group B includes the populations Niehaus (1971) determined to be tetraploid and octaploid. Therefore, Group B corresponds to *B. minor* as circumscribed by Jepson (1922) and Hoover (1939), rather than Niehaus' (1971) later circumscription.

Brodiaea nana Resurrected

The results of the morphological analysis show that *B. nana* should be recognized as a taxon distinct from *B. minor*, and on both morphological and cytological grounds, *B. nana* warrants recognition at the rank of species. Hoover (1936) originally described *B. nana* at species rank, but he later (1939) reduced it to a variety of *B. minor*, citing his observation that specimens from Sacramento County were intermediate between *B. minor* and *B. nana*. Hoover did not elaborate

TABLE 1. RESULTS OF PRINCIPAL COMPONENTS ANALYSIS ON MEANS OF ELEVEN VARIABLES FROM SIXTEEN POPULATIONS OF *B. NANA* (GROUP A) AND 20 POPULATIONS OF *B. MINOR* (GROUP B).

Variable	PC 1	PC 2
Pedicel Length	−0.251	0.428
Perianth Tube Length	0.917	0.189
Perianth Lobe Length	0.531	0.529
Width, Inner Lobe	−0.411	0.859
Width, Outer Lobe	0.088	0.925
Staminode Length	0.958	0.071
Filament Length	0.924	0.127
Anther Length	0.930	−0.024
Ovary Length	0.951	−0.025
Style Length	0.983	0.011
Ovule Number	−0.758	0.299
Eigenvalue	6.446	2.204
Variation Explained	58.60%	20.04%

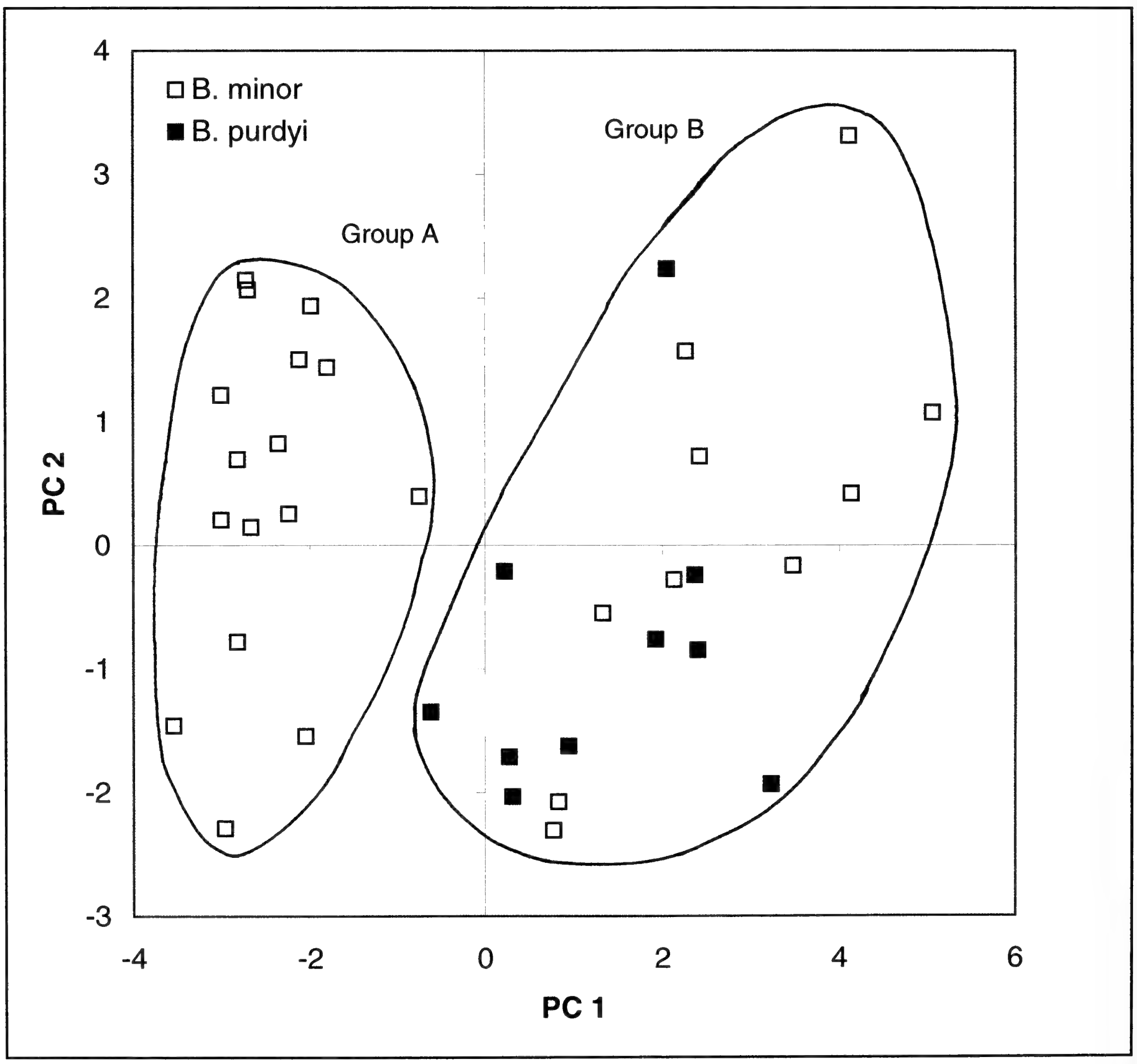

FIG. 3. Two-dimensional scatter diagram of first and second principal component scores based on population means of floral characters from *B. minor* and *B. purdyi* (*sensu* Niehaus [1971]). Group A corresponds to *B. nana* Hoover, and Group B corresponds to *B. minor* (*sensu* Jepson (1922) and Hoover (1939).

TABLE 2. COMPARISON OF FLORAL CHARACTERS FOR *BRODIAEA MINOR* AND *BRODIAEA NANA*. Measurements were made on fresh material, from one flower per plant and 10 plants per population, from 20 populations of *B. minor* and 16 populations of *B. nana*. Measurements in mm.

Character	*Brodiaea minor*		*Brodiaea nana*	
	mean	range	mean	range
Pedicel	21.4	7–45	24.5	6–56
Perianth tube	8.6	6.5–11.5	7.3	5.0–9.0
Perianth lobes	15.0	9.8–20.5	14.3	10.0–21.0
Width, inner lobes	4.7	3.0–7.0	5.5	4.0–8.0
Width, outer lobes	3.7	2.8–5.0	3.8	3.0–5.0
Staminode	9.1	6.2–12.5	7.2	6.0–9.0
Filament	2.2	1.0–3.5	1.4	1.0–2.0
Anther	5.2	3.5–7.0	4.0	3.0–5.0
Ovary	4.9	3.2–7.0	3.5	2.5–5.0
Style	8.8	6.0–12.0	5.3	4.0–7.5
Ovule number	17.3	12–24	22.2	12–33

on which features were intermediate. The ranges for all floral part measurements do overlap, but on average, all floral parts of *B. nana* are smaller than those of *B. minor* (Table 2). It is more noteworthy that the shapes of the staminodes, stamens, and pistils consistently differentiate *B. nana* from *B. minor* (Fig. 1), because *Brodiaea* species traditionally have been recognized on the basis of the shape and position of the floral parts. Recognizing *B. nana* at species rank is also consistent with Niehaus's (1971) expanded species concepts in *Brodiaea*. Niehaus's (1971) diploid chromosome counts, a major criterion for re-establishing *B. nana* at species rank (albeit as *B. minor*), were all based on populations of *B. nana* as circumscribed by Hoover and confirmed as such by the present morphological study.

The distribution of *Brodiaea nana*, documented by herbarium specimens and confirmed by visits to the collection localities, ranges from Merced County north to Chico, in Butte County (Fig. 4). In addition, several disjunct populations of *B. nana* occur on volcanic mudflows adjacent to Payne's Creek and Battle Creek, in northern Tehama County and southern Shasta County. The distributions of *B. nana* and *B. minor* overlap in Butte and Tehama Counties, but the two species are almost never sympatric. However, I collected both species growing together at one location in Chico, Butte County. *Brodiaea nana* occurs in vernal swales, shallow vernal pools, and on the margins of deeper vernal pools.

Brodiaea minor Revisited and *Brodiaea purdyi* Reconsidered

It is clear that Niehaus's (1971) concept of *B. minor* applied only to those populations circumscribed by Hoover's *B. nana*. It also clear that many of the populations Niehaus assigned to *B. minor* are morphologically indistinguishable from populations he assigned to *B. purdyi*. Niehaus's concept of two species, one consisting of diploid populations occurring in vernal pool terrain, the other of polyploid populations occurring in foothill habitats, appears to have been only partially correct, as some populations of *B. minor* occur in vernal pool terrain. Moreover, he misapplied the names when circumscribing the populations that made up the two species. How did this error come about?

First, the flowers of both species are superficially similar (Fig. 2a, c), and many of the floral parts overlap in size (Table 2). Niehaus used scape length (=10 cm = *B. minor*, =10 cm = *B. purdyi*) and petal width (5–7 mm = *B. minor*, 4–5 mm = *B. purdyi*) as key characters for separating the two species. The type of *B. minor* (*Hartweg 2002* [Isotype, NY]) has short scapes, and Niehaus evidently presumed that this population was assignable to the same taxon as Hoover's *B. nana*, and that the correct name for the taxon, therefore, was *B. minor*. However, the type locality of *B. minor* occurs in blue oak-foothill pine woodland (Hartweg 1848), not in vernal pool terrain. Moreover, scape length is not a reliable character for differentiating between *Brodiaea* taxa. Scape length varies both within and among *Brodiaea* populations and may be environmentally plastic, to some degree (Doalson 1999). The type specimen of *B. purdyi* (*Purdy s.n.* [CAS]), which illustrates this variation quite nicely, consists of three plants, one with a short scape, one with a long scape, and one with an intermediate-length scape. Petal width also overlaps between *B. minor* and *B. nana* (Table 2) and is not reliable for differentiating between them.

The results of this paper demonstrate that Niehaus's (1971) concept of *B. purdyi*, the polyploid small-flowered species, with spreading perianth lobes and floral tubes that are narrowed above the ovary, and that occurs in woodland habitats in the northern Sierra Nevada foothills, applies to the taxon originally described as *B. minor* and as recognized by Jepson (1922) and

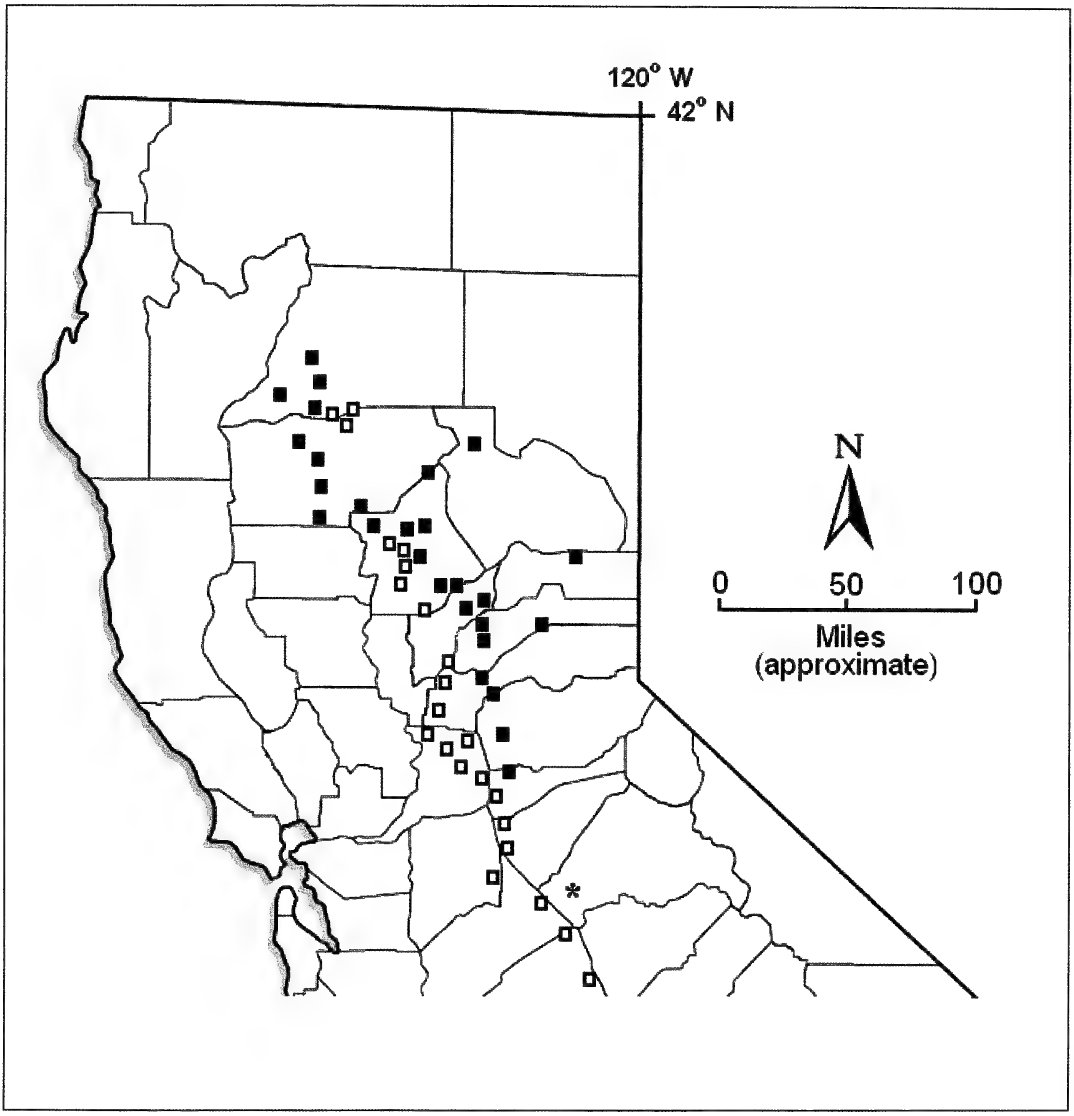

FIG. 4. Distribution of *Brodiaea minor* (■), *Brodiaea nana* (□), and *Brodiaea pallida* (*) in California, USA.

Hoover (1939), placing *B. purdyi* in synonymy with *B. minor*.

Currently, there is no basis for recognizing *B. purdyi* as a separate taxon. Eastwood (1896) noted that the original collections of *B. purdyi* were remarkable for their relatively long, narrow perianth lobes (Fig. 1d). In all other respects, however, including the shape and relative position of the floral parts, populations cannot be differentiated reliably. Moreover, there is substantial variation in perianth lobe length among populations of *B. minor*, and plants with long, narrow lobes appear to be at one end of a continuum of variation in lobe length (personal observation).

As recognized in this study and as documented by herbarium specimens, *Brodiaea minor* (including *B. purdyi*) ranges along the eastern margin of the northern Sacramento Valley, from Shasta County to Butte County, into the Sierra Nevada foothills, and south to Amador County (Fig. 4). Most populations occur in vernal pool terrain, oak woodland, or chaparral, with a few populations occurring in dry montane meadows at higher elevations. Although some populations occur on gabbro or serpentine, *B. minor* does not appear to be restricted to those substrates.

Species Relationships

Relationships between *Brodiaea* species are poorly understood. Hoover (1939) recognized a series of infrageneric groups, based on floral morphology. He proposed four informal sections,

including section "Stellares", within which he placed *B. stellaris*, *B. pallida*, and *B. minor* (including *B. nana*). Niehaus (1971) added *B. insignis* to this group. Section "Stellares" is composed of small-flowered species with rotate corollas, broad staminodes, and short filaments that are more or less channeled on the abaxial side.

The strong morphological similarity between *B. minor* and *B. nana*, as shown in this study, supports a close relationship between these two species. Niehaus (1971) found that the flavonoid chemistry and floral vasculature of the two species was also very similar. *Brodiaea pallida* and *B. nana* appear to be closely related, as well. Both species are diploid (n = 6) and have similar flavonoid chemistry (Niehaus 1971), and their ranges overlap (Fig. 4). Their floral morphology is also quite similar. The perianth tube in *B. pallida* is not or only slightly narrowed above the ovary, but in both species the staminodes are erect and the margins only slightly inrolled. The anthers have prominent abaxial papillae, the connective broadens towards the apex (see Fig. 16 in Niehaus [1971]), and the filaments are abaxially winged, although the wings in *B. nana* are not as pronounced as in *B. pallida*. Hoover (1938, 1939) discussed at length the unusual morphology of the staminodes and stamens in *B. pallida*. His statement that these features were quite different from those of *B. minor* and his later treatment of *B. nana* as a variety of *B. minor* suggests that he was unaware of the similarities between *B. pallida* and *B. nana*.

Brodiaea stellaris and *B. insignis* appear to be less closely related to *B. nana, B. minor* and *B. pallida*. Flowers of *B. insignis* are at least superficially similar to those of *B. nana* and *B. minor* (unpublished data), although the floral tube is not constricted and the chromosome number (n = 16) and flavonoid compounds are substantially different than those two species (Niehaus 1971). In contrast, *B. stellaris* is a diploid (n = 6) with similar flavonoid chemistry to *B. nana, B. minor*, and *B. pallida*, but it is morphologically quite different from these species. Hoover (1939) originally grouped *B. pallida* with *B. stellaris* because the filaments of both species are prominently winged abaxially. In most other respects—shape of the perianth tube and lobes, staminodes, stamens, and ovary, and the relative proportion of these floral parts—*B. stellaris* is very different (unpublished data).

The following key to the species of section "Stellares" serves to differentiate between the species.

1a. Staminodes hooded at the tips, the margins not or only slightly incurving, connate at the base with the stamens; filaments with prominent apical appendages abaxially; North Coast Ranges, on serpentine . . . . *B. stellaris*
1b. Staminodes not hooded at the tips, the margins incurving to strongly inrolled, not connate at base with stamens; lateral margins of filaments winged, but appendages lacking.
2a. Perianth tube not narrowed above the ovary; filaments dilated at base; style shorter than ovary; southern Sierra Nevada foothills . . . . *B. insignis*
2b. Perianth tube narrowed above the ovary; filaments not or only slightly broader at base than at apex; style longer than the ovary.
3a. Staminodes erect to spreading, margins strongly inrolled; stamens narrowly notched at apex, lacking prominent papillae abaxially; filaments winged laterally, T-shaped in cross-section . . . . *B. minor*
3b. Staminodes erect, margins not to slightly inrolled; stamens broadly V-shaped at apex, with prominent abaxial papillae; filaments winged abaxially, V- or Y-shaped in cross section.
4a. Perianth lobes paler towards the base; perianth tube slightly narrowed above the ovary; staminodes as broad as or broader than the outer perianth lobes; central Sierra Nevada foothills, in swale, serpentine soil . . . . *B. pallida*
4b. Perianth color uniform; perianth tube strongly narrowed above the ovary; staminodes narrower than outer perianth lobes; eastern edge of Central Valley, in vernal pools and swales . . . . *B. nana*

Questions for Further Study

Although this study may have resolved the taxonomy of *B. minor* and *B. nana*, many phylogenetic questions remain. *Brodiaea minor* consists of populations of both tetraploids and octaploids. Niehaus (1971) postulated that *B. minor* was derived from diploid *B. nana*. Whether *B. minor* was derived via autopolyploidy or allopolyploidy is unclear. Whether octaploid *B. minor* was derived from *B. nana* or from tetraploid *B. minor* is also unclear. Moreover, the possibility exists that *B. minor* is a complex of polyploid populations of multiple origins, rather than a tetraploid lineage and an octaploid lineage.

The relationships between *B. pallida, B. minor*, and *B. nana* and other *Brodiaea* species remain uncertain. Reliance on morphological data alone has proved of limited usefulness in resolving relationships between and among *Brodiaea* species. Although groups of species can be recognized on the basis of unique characters, the phylogenetic relationships among the groups are still ambiguous. Niehaus (1971) provided some cytological, anatomical, and flavonoid data that may provide evidence for elucidating relationships, but little has been done to follow up on Niehaus's work. Niehaus's suggestion that eco-

logical data might be useful has also not been pursued.

Recent studies based on molecular data have proved useful for understanding relationships within the Themidaceae and may point a way towards resolving species relationships within *Brodiaea* (Pires and Sytsma 2002). Independent data sets derived from molecular data may help determine which morphological characters are plesiomorphic, which are derived, and which, like the "winged" filaments of *B. stellaris* and *B. pallida*, may be homoplasic. Molecular data may also be useful for differentiating between entities that have been derived via autopolyploidy or allopolyploidy (Rieseberg and Ellestrand 1993). *Brodiaea* remains a nearly untapped source for investigations on polyploidy, hybridization, and edaphic relationships.

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FACTORS AFFECTING UNDERSTORY ESTABLISHMENT IN COASTAL SAGE SCRUB RESTORATION

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ABSTRACT

Coastal sage scrub (CSS) is a target for restoration because it provides habitat for numerous special-status species and it has been impacted by urbanization, agriculture and invasion by non-native species. Many restoration designs have neglected the herbaceous understory component of CSS, although it may comprise the majority of vascular plant species in a natural CSS stand. The omission of an understory may promote invasion by non-native plants and reduce overall success. This study investigated the role of native seed addition, non-native species removal, gaps in the shrub canopy, and soil moisture, upon establishment of a native understory. Native biomass increased significantly with seed addition, and the abundance of experimentally seeded native species was positively correlated with soil moisture. Natives were not affected by competition with non-natives or the presence of gaps. Although all seeded native species germinated, only two of seven established successfully, perhaps due to very low rainfall. Non-native species were negatively affected by the addition of native seeds and had greater growth in gaps. We conclude that planting shrubs in a dense configuration to reduce gap size may reduce non-native species abundance in the understory while having little effect on the native understory. Seeding may be all that is required to establish a native understory, and may also be an effective method of suppressing non-native species.

Key Words: coastal sage scrub, restoration, competition, invasive species, seed limitation.

Coastal sage scrub (CSS) is one of the most endangered habitats in southern California. Estimates of CSS loss vary, however it is likely that CSS currently occupies less than half of its historical distribution (Westman 1981; O'Leary 1995). Primary causes of CSS loss are urbanization, agriculture, and the degradation and replacement of natural stands by the invasion of non-native species, mostly annual grasses from the Mediterranean region (Freudenberger et al. 1987; O'Leary and Westman 1988; O'Leary 1995; Minnich and Dezzani 1998). These ecosystem stressors, as well as the importance of CSS as habitat for numerous rare, threatened, or endangered plants and animals, make the community a priority for conservation (Davis et al. 1994). Regional multi species habitat conservation plans throughout southern California anticipate additional loss of CSS and require both preservation and restoration of CSS to mitigate for this loss. Thus, development is resulting in increasing numbers of CSS restoration sites, making successful restoration strategies essential for effective CSS conservation.

Typical CSS has a dense shrub canopy 0.5–1.5 m in height and a sparse herbaceous understory of primarily annual species concentrated in gaps between shrubs. Invasive non-native species are increasingly common in CSS understories (O'Leary 1995). Non-natives are undesirable in restoration projects because they reduce the success of planted shrubs (Eliason and Allen 1997) and compete with native understory herbs. Although many restoration designs target only the native shrub canopy, restoration of the understory as well is a more logical approach (Bowler 2000). Thus, understanding the ecological factors controlling understory structure and composition is important.

Previous studies have suggested numerous mechanisms involved in competition between non-native and native plant species. Competition with non-native annual grasses for soil moisture often limits the success of native perennials (Melgoza et al. 1990; Eliason and Allen 1997; Humphrey and Schupp 2004; but see Seabloom et al. 2003a). Competition with non-natives for soil moisture could also have an impact upon native understory annuals, although this has not been directly tested in CSS. Reduced light availability beneath shrubs may also reduce understory growth, resulting in a relatively higher density of understory plants in gaps, and shading from non-native grasses growing in gaps may affect these native plants (Thompson and Harper 1988; Dyer and Rice 1999).

Coastal sage scrub understories share many species with California's coastal grasslands. In two coastal grassland experiments in California, Seabloom and colleagues found that native perennial grasses (2003a) and annual forbs (2003b) were strongly seed-limited. Following seed addition, natives successfully established despite competition from non-natives. These

TABLE 1. SEEDING DENSITY, % EMERGENCE, AND RELATIVE SUCCESS OF NATIVE ANNUAL PLANTS ADDED. Biomass values (±1 SE) were calculated from seed addition plots only. Seed emergence data were obtained from S&S Seeds (Carpinteria, CA).

Species	N seeds added/plot	% Seed Emergence	Mean end of season biomass (g m^{-2})
Amsinckia menziesii (Boraginaceae)	280	54	0.38 ± 0.15
Cryptantha muricata (Boraginaceae)	990	26	0.00
Lasthenia californica (Asteraceae)	6240	80	8.03 ± 2.31
Lepidium nitidum (Brassicaceae)	970	51	0.00
Plantago erecta (Plantaginaceae)	360	88	0.00
Lupinus bicolor (Fabaceae)	190	85	0.00
Lupinus truncatus (Fabaceae)	60	91	0.00

results suggest that seed limitation also could explain the failure of many restored CSS communities to develop a native understory.

This experiment's objective was to identify the primary factors limiting establishment of native understory herbs during CSS restoration. Limitation likely results from several interacting factors. Through an experimental restoration, we addressed the following four questions: 1. Is seed addition alone sufficient to restore a CSS native understory? 2. Do non-native and native understory plants compete with one another? 3. Does the reduced light environment beneath mature shrubs reduce the growth of understory plants? 4. Does soil moisture affect native understory establishment and competition with non-natives?

METHODS

Site Description

This experiment was conducted on an existing CSS restoration site adjacent to the University of California, Irvine Arboretum and UC Natural Reserve System's San Joaquin Freshwater Marsh Reserve. Prior to restoration in 2002, this site was an abandoned agricultural field that had no resident native taxa and was dominated by non-native species including *Brassica nigra* (Brassicaceae), *Foeniculum vulgare* (Apiaceae), *Cynara cardunculus* (Asteraceae), and annual grasses, primarily of the genus *Bromus*. (Nomenclature follows Hickman 1993) These same species dominated the area surrounding the site. Annual rainfall in the area is approximately 300 mm yr?¹.

During October–November 2002, *Artemisia californica* (Asteraceae) shrubs were planted in circular clusters approximately 3 m in diameter. Shrubs were planted at an average density of 2.5 plantings m^{-2}. To minimize mortality during establishment, plantings were watered weekly until February 2003, and were hand-weeded during the first spring (2003). No herbicides were applied at any time during restoration.

Experimental Design

This experiment was conducted during February–May 2004, 1.5 years after the *A. californica* clusters were planted. Native propagule abundance was manipulated by adding native seeds of five native annual forbs and two annual legumes (Table 1). Presence of non-native species was manipulated by clipping all non-native species at ground level. Seed addition and non-native removal were combined in all possible combinations, resulting in the following four plot types: 1. Native seeds added, non-native species removed; 2. Native seeds added, no removal; 3. No seed addition, non-native species removed; and 4. No seed addition and no removal.

Experimental plots were situated a minimum of 25 cm from the edge of each *A. californica* cluster and from other plots. The plots were 50 cm × 50 cm, with treatments extending an additional 10 cm beyond the plot boundary. Plot locations were assigned randomly within eight replicate blocks, each of which was located within a single cluster of shrubs and included all four treatment combinations. Within blocks, plot orientations were assigned non-randomly to include a single shrub immediately outside the plot at one end and a gap in the shrub canopy (no shrub canopy directly overhead) at the other end. This plot orientation allowed investigation of the importance of gaps in the distribution of understory herbs beneath a CSS canopy. Each plot was divided into two 25 cm × 50 cm subplots: one under the canopy and one in the adjacent gap.

Experimental Treatments

Seed addition. We amended plots with seed from five native annual forb and two annual legume species at a density of 4.5 g m^{-2} per taxon (Table 1). All seeds were obtained commercially from S&S Seeds (Carpinteria, CA). Plots were seeded on 19 February 2004. Prior to seed addition, the soil was disturbed by hand-raking to a depth of 2 cm. Control plots were similarly disturbed. After seed addition, the loosened soil

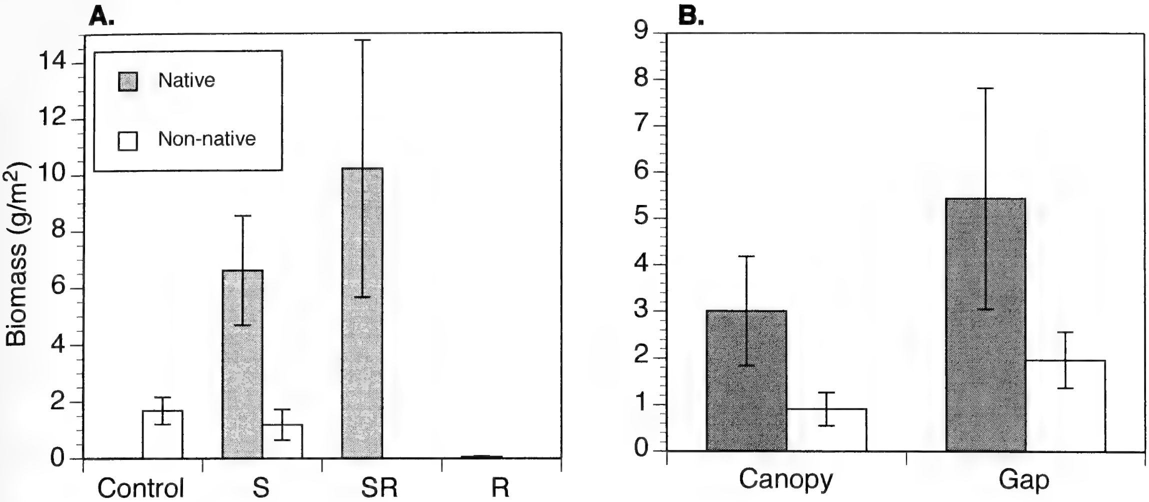

FIG. 1. Biomass of native (shaded bars) and non-native (open bars) species in (A): plots with native seed addition only (S), seed addition and non-native species removal (SR), non-native species removal only (R), and no treatment (control), and (B): subplots beneath the shrub canopy and in gaps. In control and R plots, *Artemisia californica* was the only native present. In S and SR plots, most of the native biomass was from *Lasthenia californica*. Bars are means ± 1 SE.

was spread over the seeds to minimize losses from wind, runoff, and predation. Because rainfall was below average during the experiment, supplemental water was provided in late March and early April to prevent excessive mortality.

Seeded species were harvested on 12 May 2004, at the end of the growing season. To determine if seed addition had an effect on any preexisting native understory, all volunteer native species were collected as well. Aboveground biomass was dried for 48 hr at 60°C and weighed.

Non-native species removal. All non-native species were removed from weeded plots by clipping at ground level. Early germinating species were removed on 9 March, as soon as plants were identifiable. A second removal was performed on 1 April to remove later germinating species. No non-native species were observed in any weeded plots after the second removal. Non-natives from unweeded plots were harvested, dried, and weighed with native species at the end of the growing season.

Soil moisture and light availability. Photosynthetically active radiation (PAR) was measured in each subplot within 2 hr of solar noon on 29 April. Values were recorded as the ratio of light measured below the canopy to incident light measured directly above the canopy. Soil moisture in the top 12 cm of soil was also recorded using a Hydrosense TDR probe (Campbell Scientific, Logan, UT). Deeper readings were not taken to avoid excessive disturbance within the plots and because the rocky soil made probe insertion difficult. Three soil moisture readings were taken from each subplot, and the results were averaged prior to analysis. Soil moisture was recorded on 11 May, one day prior to harvesting all aboveground biomass in the plots.

Statistical Procedures

To meet assumptions of normality and homogeneity of variance, a natural log transformation on all biomass measurements was performed, and soil moisture measurements were rank transformed. Because light intensity measurements were normally distributed, they were not transformed.

To determine how shrubs influenced light and soil moisture, a paired t-test was conducted to compare light intensity between canopy and gap subplots, and a Wilcoxon signed rank test was used to test for a soil moisture difference between subplot types.

We used analysis of covariance to examine effects of seed addition, non-native removal, light, and soil moisture on the biomass of native herbs. A similar analysis was used to test effects of native seed addition, light, and soil moisture on non-native biomass within non-removal plots.

RESULTS AND DISCUSSION

Native Seed Addition

Native seed addition significantly increased native understory biomass. Native biomass in seed addition plots averaged 8.41 ± 2.45 g m^{-2}, compared to 0.03 ± 0.02 g m^{-2} in control plots ($F_{1,50}$ = 310, P < 0.001; Fig. 1a). Natives averaged 2.6% of total herbaceous biomass in

unseeded, unweeded plots and 88.5% in seeded, unweeded plots.

Although all seven seeded species were observed germinating, only *Lasthenia californica* (Asteraceae) and *Amsinkia menziesii* (Boraginaceae) survived long enough to produce flowers (Table 1). *Lasthenia californica* produced 98% of native biomass, while *A. menziesii* produced the remaining 2%. The only volunteer natives observed were *A. californica* seedlings.

No substantial populations of native CSS herbs were observed within several hundred meters of the study site, and it is likely that seed dispersal beyond this distance is very low (Van Dorp et al. 1996; Jongejans and Schippers 1999). Furthermore, the absence of any native herbaceous growth in unseeded plots suggests that no native seed bank remained on the site. Past disturbance and several decades of non-native species dominance has likely eliminated any native seed bank that may have been present. Because an impoverished native seed bank and few local seed sources may be typical of many potential CSS restoration sites, seed addition of understory herbaceous plants is likely to be a necessary component of many restoration projects.

Competition

In unweeded plots, native seed addition caused a small but significant decline in non-native biomass, from 1.68 g m^{-2} to 1.19 g m^{-2} ($F_{1,20}$ = 4.76, P = 0.04; Fig 1a). The small magnitude of this change is likely due to low non-native biomass throughout the planted area. The high biomass of *L. californica* in seeded plots suggests that this species, if seeded at high densities, may be effective at controlling non-native species.

There were no significant effects of non-native removal on native biomass, regardless of seeding treatment. However, due to low non-native biomass and low survival of most seeded native species, it is difficult to make any conclusions about a competitive effect of non-native species on natives. Strong competitive effects of non-native species in CSS and similar systems have been demonstrated in the past, and may have been observed in this system had non-natives been more abundant (D'Antonio and Vitousek 1992; Eliason and Allen 1997; but see Seabloom et al. 2003b).

Shrub Effects

As expected, light intensity was significantly lower beneath the canopy (mean 47 ± 3.0%) than it was in gaps (74 ± 3.0%). There was no significant difference in soil moisture between canopy and gap subplots. Native understory biomass did not differ significantly between the shrub canopied and gap plots, suggesting that any competitive effect of shrubs on the natives may have been balanced by a facilitative effect. Non-native biomass was significantly less beneath the canopy ($F_{1,20}$ = 5.80, P = 0.03; Fig. 1b). This was likely due to the large reduction in light intensity beneath the canopy, although it may also be due to belowground effects not measured in this study.

Soil Moisture

There was a significant positive relationship between soil moisture and native biomass ($F_{1,50}$ = 5.54, P = 0.02), but not between soil moisture and non-native biomass. Although soil moisture was limiting for both natives, the importance of soil moisture may have been exaggerated by the very low precipitation throughout the growing season. Low soil moisture may also explain the high mortality observed for most seeded native species. These species were observed germinating, but died during mid-season when rainfall also declined sharply below weekly averages. Finally, the lack of a difference in native growth between low light (canopied) and high light (gap) subplots would be expected if soil moisture was more limiting than light, and shading by shrubs reduced water stress for the native understory.

Conclusions

This study suggests that in restored dense-canopy CSS, soil moisture is an important limiting factor for native understory species, while light is more limiting for non-natives. Non-natives were also more abundant in gaps than they were beneath the shrub canopy, suggesting a competitive effect of the shrubs. Thus, the presence of a mature, dense shrub layer may effectively exclude a large fraction of non-native species without adversely affecting some native species.

Competition with the restored native understory (which consisted primarily of *L. californica*) significantly reduced non-native biomass. Thus, the addition of seeded native understory herbs may be an effective secondary restoration strategy, particularly given that long distance dispersal of native understory herbs is likely to be a rare event. Seeding may be accomplished at a fairly low cost and can successfully establish some native herbs and reduce the abundance of non-native species.

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OBSERVATIONS OF FROND GROWTH AND DEVELOPMENT IN *PENTAGRAMMA TRIANGULARIS* SUBSP. *TRIANGULARIS* (PTERIDACEAE) OF SOUTHERN CALIFORNIA

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ABSTRACT

Frond growth and development of *Pentagramma triangularis* subsp. *triangularis* was examined in canyon populations in Ventura County, California during the winter growing season of 2003. Fronds developed from emerging croziers to full size within 35 days and reached sexual maturity by 70 days. Frond growth occured in two stages with stipe elongation nearly complete when the crozier began to unfurl, about a week before full maturation of the entire frond. Discernable developmental stages are described as well as their respective ages. Fern growth occurred both prior to and after the study frond monitoring period, indicating multiple growth flushes throughout the growing season, possibly related to rain events. Based on these preliminary results, suggestions are offered for further study.

Key Words: frond growth, *Pentagramma triangularis*, phenology, Pteridaceae, southern California.

Pentagramma triangularis (Kaulf.) Yatsk., Windham & E.Wollenw. (Pteridaceae) grows in western North America (Yatskievych and Windham 1993) inhabiting rock crevices within a variety of habitats including woodlands, chaparral and deserts (Smith 1998). Plants of this species complex, commonly called goldback and silverback ferns, produce 10–35 fronds (7–40 cm) from a short, slender rhizome. Each frond consists of a brown to black stipe and a deltate-pentagonal, 1–2 pinnate-pinnatifid blade as wide as long (4–9 cm). The abaxial surface of blades are covered with silver or gold farina, hence their common names. Plants are winter-green perennials producing fronds at first rains, which persist until hot weather, when their blades curl due to drought (Yatskievych et al. 1990; Smith 1998).

The ecology and life history of these ferns are largely unexplored. Except for having a growing season that coincides with winter rains, frond phenology of *P. triangularis* is largely undocumented. This lack of knowledge regarding frond phenology is representative of the pteridophytes in general, with few studies reported in the literature (e.g., Sato 1982; Willmot 1989; Sharpe and Jernstedt 1990; Johnson-Groh and Lee 2002).

The objectives of this study were to measure the growth and to describe the developmental stages of *P. triangularis* subsp. *triangularis* fronds. This report presents the first detailed phenological description for *Pentagramma* and lays a foundation for further study of *P. triangularis* life history, which could provide a better understanding of this fern's adaptation to its seasonally dry habitat.

METHODS

Pentagramma triangularis subsp. *triangularis* ferns were monitored in two small populations along the Cozy Dell Trail in Sheldon Canyon, Ventura County, California (34°28′39″N, 119°17′09″W). The study area, located 22 km from the coast at an elevation of 427 m, is in the Transition Climate Zone and is influenced by a mixture of maritime and continental air masses with hot, dry summers and mild, rainy winters (Bailey 1966; Hickman 1993). Total rainfall for the 2002–2003 rainy season (from October through April) in Stewart Canyon, 3.2 km ESE of the site, was 454 mm with most falling in November, December and March. Temperatures taken at Matilija Dam, 2.4 km WNW of the study site for the same period, included a winter minimum of 6.3°C in December and spring maximum of 22.8°C (Ventura County Watershed Protection District, unpublished data). However, this rainy season was atypical in being warm, with a dry spell in January (Fig. 1).

The study area is a steep, north-facing slope with cobble and boulder talus of sedimentary rocks (Norris and Webb 1990) in coastal oak woodland/mesic chaparral dominated by a patchy canopy of *Quercus agrifolia* Née (Fagaceae) with a dense shrub layer of *Ceanothus cuneatus* (Hook.) Nutt. (Rhamnaceae) and *Heteromeles arbutifolia* (Lindl.) M. Roem. (Rosaceae). Understory seed plants included *Toxicodendron diversilobum* (Torr. & A. Gray) Greene (Anacardiaceae), *Diplacus* (=*Mimulus*) *longiflorus* Nutt. (Phrymaceae), and undetermined grasses and forbs. Other ferns in this area included *Polypodium glycyrrhiza* D.C. Eaton (Polypodiaceae),

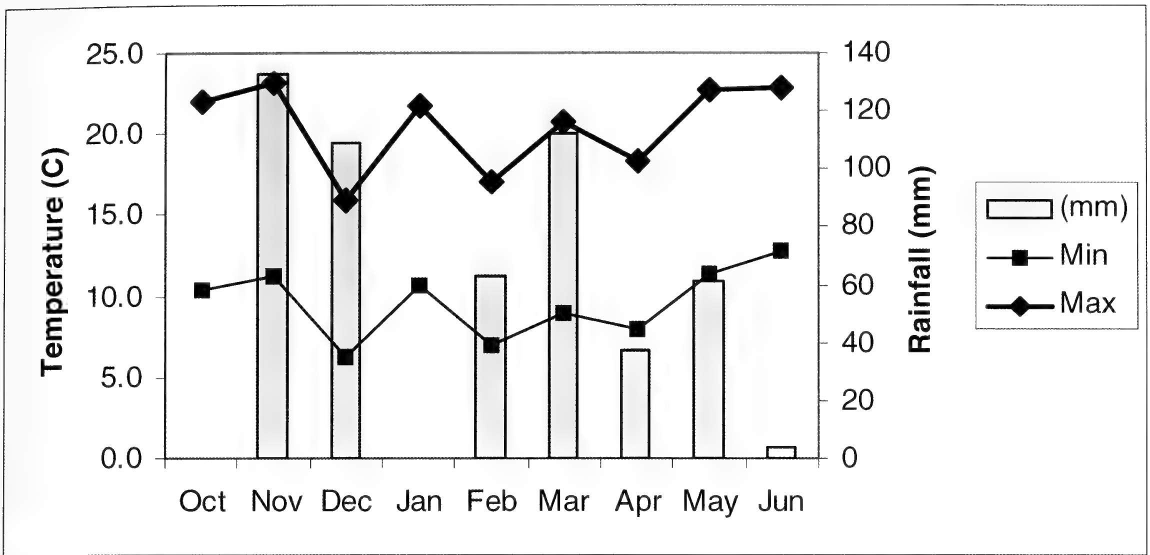

FIG. 1. Rainfall and temperature patterns for the October 2002–April 2003 rainy season, extended to June 2003, at Stewart Canyon and Matilija Dam meteorological stations, respectively (data source: Ventura County Watershed Protection District).

Pallea andromediflora (Kaulf.) Fée (Pteridaceae), and *Dryopteris arguta* (Kaulf.) Maxon (Dryopteridaceae). Exposed rock surfaces harbored *Selaginella bigelovii* Underw. (Selaginellaceae) plus foliose and crustose lichens.

The study populations, separated by 0.2 km, consisted of 24 and 25 ferns each, with densities of approximately 1.6 and 6.3 ferns m^{-2}, respectively (densities appeared determined by amount of rocky edge microhabitat). Ten ferns per population were haphazardly selected for study. Data from the two populations were lumped for analysis because no significant differences were observed between them.

On 5 January 2003, I selected for study the crosier on each fern that was closest to the soil surface ($\leq$10 cm height), and thus recently emerged, and marked its stipe with correction fluid for growth monitoring. Weekly measurements of marked fronds included stipe and rachis lengths (while in crozier, head diameter was measured to represent this variable); for developmental stage classification, the frond's development (i.e., shape, color, farina, and presence of sporangia) was also described. Lengths were measured until fronds had reached their full size (i.e., no increase for three consecutive measurements), but developmental observations continued until the frond senesced. Three fronds failed to grow and develop completely, and for these a replacement crosier on the fern was marked and monitored. Two of these were on one plant that senesced prematurely, in March; this fern was on an exposed rockface.

Growth curves were developed from the stipe and rachis length means. Other phenological observations of these plants were also made at irregular intervals, including after the period of frond growth monitoring. Voucher specimens were deposited at Santa Barbara Botanic Garden Herbarium (SBBG).

RESULTS

Frond Growth and Development

From 5 January through 26 March 2003 development of study fronds passed through seven discernable stages from crozier to mature sporophyll. Growth curves are shown in Figure 2, while the mean ($\pm$1 SD) frond sizes and their respective percent mature sizes for each developmental stage are listed in Table 1 and included in the text below. Frond stages are described below.

(1) Young Crozier (YC): Fronds first appeared light green, with stipe lengths from emergence (0 cm) to 5.5 cm. Crozier diameters averaged 0.32 $\pm$ 0.11 cm.

(2) Mature Crozier (MC): Stipe lengths averaged 9.3 $\pm$ 3.7 cm or 64 $\pm$ 16% of the full length and darkened from the base toward the tip. Croziers grew to 0.44 $\pm$ 0.14 cm diameter with pinnae visible. Fronds were in this stage for 7–14 days.

(3) Unfurling Frond (UF): Blade development began with croziers opening at 14–28 days after emergence, lasting seven days or less. Stipes elongated on average to 94 $\pm$ 4% of their mature length and rachises reached a mean of 30 $\pm$ 9.5% of mature size.

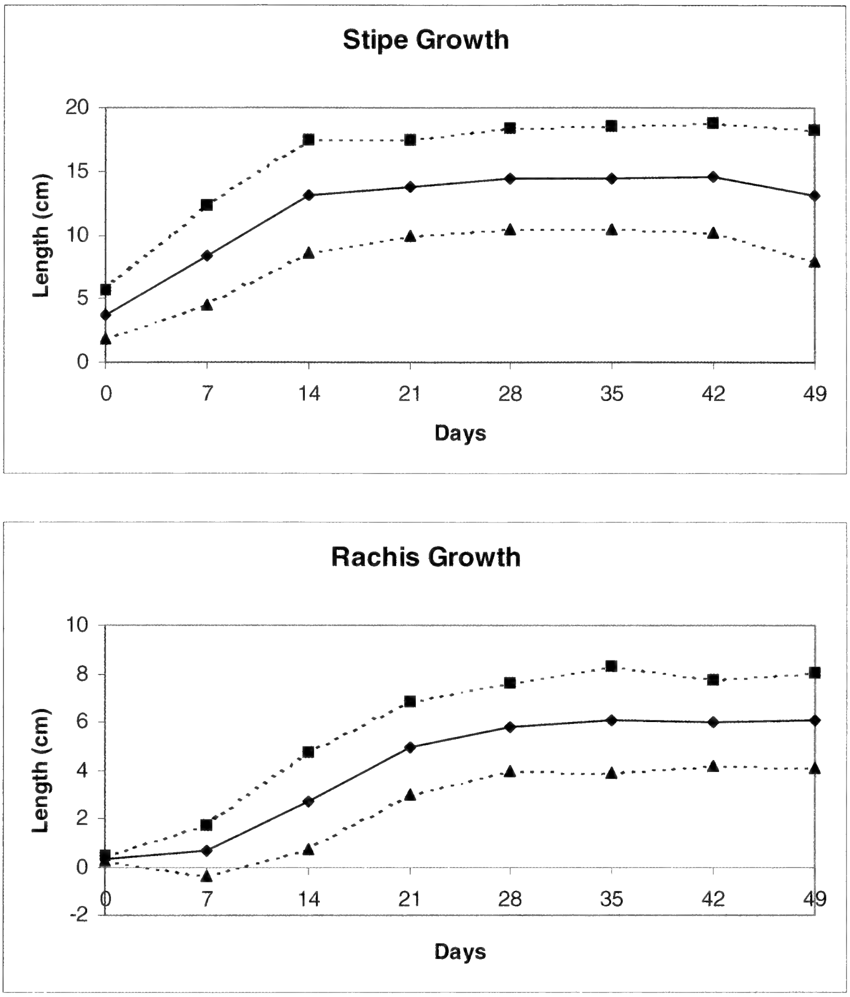

FIG. 2. Mean (± 1 SD) growth curves of frond stipes and rachises from 18 *Pentagramma triangularis* subsp. *triangularis* ferns monitored in Sheldon Canyon, California, USA during 05 January–16 March, 2003.

(4) Immature Frond (IF): By 7–21 days, blades were fully open at this stage with thin shiny, yellowish green pinnae and pinnules that expanded as the blade developed. Stipes reached their full length while rachises elongated to an average of 80 ± 15% (range 53–100%) of full size.

TABLE 1. MEAN ± 1 SD LENGTHS PLUS PERCENT OF MEAN MATURE SIZES OF *PENTAGRAMMA TRIANGULARIS* SUBSP. *TRIANGULARIS* FROND DEVELOPMENTAL STAGES. Observations made in Sheldon Canyon, Ventura County, California, USA, 05 January–16 March with Sporophyll Observations until 01 June 2003. Number of observations included multiple examinations of 18 monitored ferns (one frond per plant). Monitoring of stipe growth ceased once fronds reached full size. See text for stage definitions.

Stage	Frond age (Days)	Stipe		Rachis		No. Observations
		Length (cm)	% Mature	Length (cm)	% Mature	
YC	0–7	3.3 ± 1.6	26 ± 9	0.3 ± 0.1	6 ± 1	8
MC	< 7–14	9.3 ± 3.7	64 ± 16	0.4 ± 0.1	8 ± 2	16
UF	14–28	13.1 ± 4.3	95 ± 6	2.0 ± 1.1	30 ± 9	8
IF	14–35	14.7 ± 3.5	100	5.0 ± 1.5	81 ± 16	25
MF	21–63	14.4 ± 4.3	100	5.9 ± 1.8	100	56
IS	63–77	N/A	N/A	N/A	N/A	14
MS	70+	N/A	N/A	N/A	N/A	48

(5) Mature Frond (MF): Blades developed a dull green color with light farina abaxially by 21–35 days. During frond maturation some stipes developed a bent stature.
(6) Immature Sporophyll (IS): Sporangia were first observed at 56–70 days as a light brown dusting on the abaxial surface.
(7) Mature Sporophyll (MS): Fronds appeared dark green adaxially; farina were mixed with dark brownish sporangia on the abaxial surface. Growth-monitored fronds were first observed in this stage by 63–77 days.

Not all crosiers were of equal length at the start of monitoring, thereby lowering precision of this growth study. By 26 July, 175 days after monitoring began, all study fronds had curled adaxially in senescence, exposing the farinose abaxial surface.

Duration of frond (i.e., stipe and rachis) growth averaged 19.8 ± 5.7 days. Stipe elongation averaged 12.4 ± 5.3 days, which was a significantly shorter growth period than for the frond entire (t-test, $P = 0.0004$). Growth duration of the rachis was equivalent to growth duration of the frond entire, because it included rachis growth while in the crosier head.

Phenology

At the onset of this study (5 January 2003), ferns had young as well as older fronds, the latter already in the mature sporophyll stage. On 15 December 2002, ferns in the area also were observed exhibiting the full range of frond developmental stages from young crosier to mature sporophyll. During this study, crosiers appeared on the study plants as late as 23 March, when most of the growth-monitored fronds were already in the mature sporophyll stage. Young crosier observations appeared to follow rain events of >50 mm within approximately 14 days, but data were insufficient for statistical analysis. By 26 July, however, all fronds on plants in the study area had senesced.

Discussion

The growth of monitored fronds was completed within 35 days; reproductive maturation of fronds was completed within 70 days. Frond development passed through a series of discernable stages, which are useful for describing a frond's growth and reproductive state. Observations of older fronds at later stages growing concurrently with younger fronds indicated that frond production and growth occurs in successive flushes. Determining how many flushes of new fronds can occur within a season and how they are triggered will probably require observations over several years, especially considering the variable nature of the southern California climate (Nilsen and Muller 1981).

While this note describes the frond growth, development and phenology in *P. triangularis* subsp. *triangularis*, the results are based on observations at a single site during only part of one year; thus, further study is needed to confirm and elaborate on these findings. In particular, populations should be monitored for consecutive years, and observations of reproductive development should include microscopic examination of freshly collected sporophylls. Questions for future investigation include: 1) what environmental factors (e.g., rain, temperature, daylength) trigger onset of fern growth and how quickly do ferns respond to these factors; 2) do flushes of growth coincide with periodic rain events within a season, and if so, how many flushes can occur in a year; 3) how long is the growing season for this species, and how long do individual fronds live before senescence;, 4) what triggers sporulation, and how long is sporangial development prior to sporulation; 5) how does habitat and microhabitat affect the phenology; and 6) how does the phenology of *P. triangularis* subsp. *triangularis* compare with that of co-occurring fern taxa.

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HABITAT, GEOLOGIC, AND SOIL CHARACTERISTICS OF SHASTA SNOW-WREATH (*NEVIUSIA CLIFTONII*) POPULATIONS

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ABSTRACT

Following our recent discovery of seven new Shasta snow-wreath populations during 2003 and 2004, we conducted a GIS analysis using location data from the new sites, and from all previously known sites to determine the habitat, geologic, and soil characteristics of each Shasta snow-wreath population location. Previously considered a species only associated with limestone substrates, our new information shows that 47% of all known Shasta snow-wreath sites occur on non-limestone geologic or soil types.

Key Words: Shasta snow-wreath, *Neviusia cliftonii*, limestone, Shasta Lake, geology, soil, Rosaceae.

Shasta snow-wreath (*Neviusia cliftonii* Shevock, Ertter & Taylor) is a recently discovered shrub of the Rosaceae: Kerrieae. It is endemic to northern California in the vicinity of Shasta Lake, Shasta County. The environmental conditions and geographic isolation of the species suggest that it is one of the remnant taxa of an old, formerly more widespread genus (Shevock et al. 1992). A fossil occurrence of a closely related plant in a Pacific Northwest Eocene flora supports this hypothesis (DeVore et al. 2004).

The species' type locality and the subsequent two populations discovered were on limestone substrates (Shevock et al. 1992; Taylor 1992; Shevock 1992). Shasta snow-wreath was therefore thought to represent a limestone endemic species, and is described in *The Jepson Manual* (Hickman 1993) as a species occurring in habitats associated with limestone rock formations. Its closest relative, *Neviusia alabamensis* Gray, of the southeastern U.S., commonly occurs on limestone, but is also found on sandstone and shale substrates (Yocom and Little 1975; Patrick et al. 1995). Subsequent observations of Shasta snow-wreath in the Shasta Lake area demonstrate that it too occurs on soils of non-carbonate origin.

PREVIOUSLY KNOWN OCCURRENCES

The California Department of Fish and Game's California Natural Diversity Database (CNDDB) and the California Native Plant Society Inventory of Rare and Endangered Plants contain records of ten known Shasta snow-wreath locations (excluding the new locations discussed in this article). Habitat information reported for these ten previously known locations indicates that eight (80%) occur within habitats associated with limestone rock formations. Most of those first ten Shasta snow-wreath discoveries were made during the year following the initial type locality discovery and publication of the species name, when efforts to find additional Shasta snow-wreath occurrences focused on other limestone areas near Shasta Lake as potentially suitable habitat (Shevock 1992).

NEW OCCURRENCES

During field investigations in 2003 and 2004, North State Resources, Inc. personnel discovered seven new Shasta snow-wreath locations in the vicinity of Shasta Lake (Lindstrand and Nelson 2004) (Fig. 1). Specifically, these discoveries occurred during vegetation and habitat mapping conducted along the margins of Shasta Lake, and were opportunistic discoveries, rather than results of a systematic plant survey. These new locations occur primarily along drainages in dense, shady montane hardwood-conifer and ponderosa pine forests, but also in open foothill pine-blue oak woodland habitat. The new snow-wreath populations range in size and aerial extent from several plants in a relatively small area, to extensive stands consisting of thousands of plants blanketing both sides of a stream corridor for at least a quarter mile. Of these seven new occurrences, only one is associated with limestone substrate.

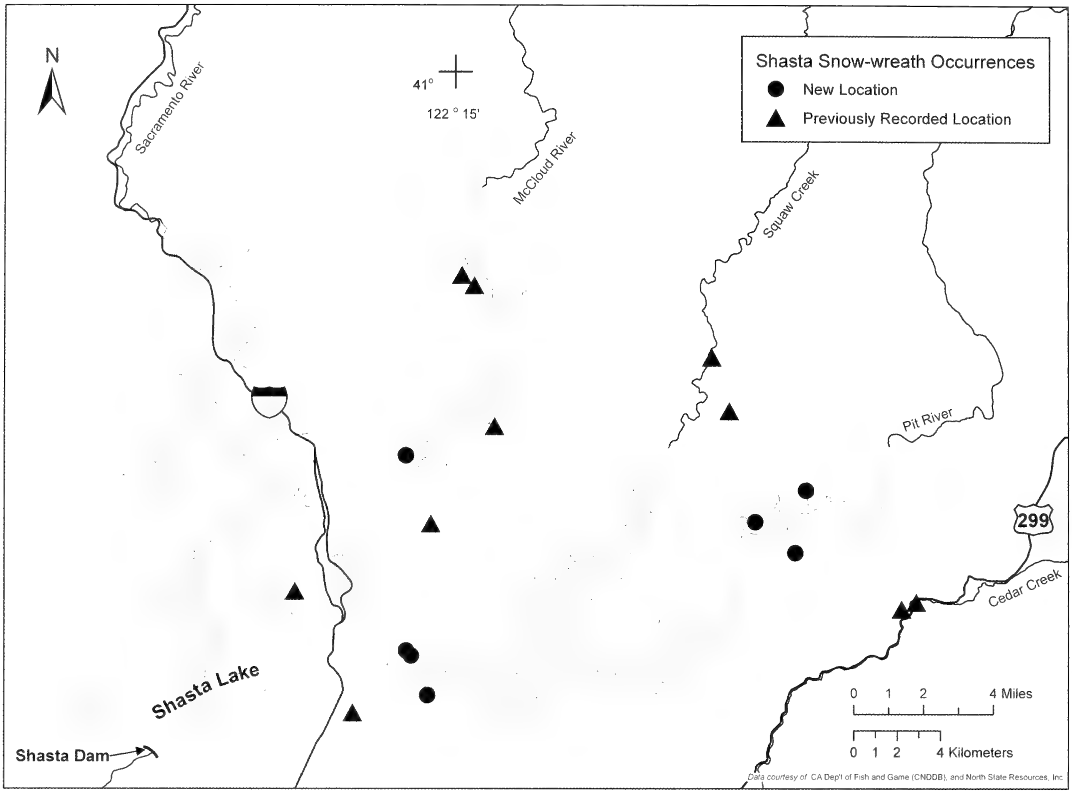

FIG. 1. Known Shasta snow-wreath occurrences and distribution. Shasta County, California.

Analysis of Geology and Soil Characteristics

A geographic information system (GIS) analysis of all known Shasta snow-wreath occurrences was performed in order to quantify the distribution of occurrences on carbonate and non-carbonate substrates. All ten previously documented occurrences listed in the CNDDB were extracted to a GIS shapefile as point data. We then converted our seven new occurrences to point data and added that data to the shapefile. The shapefile was intersected with a digital geologic map of the Shasta Lake area (USDA Forest Service 2004), and the distribution of Shasta snow-wreath occurrences by geologic map unit and general geologic type was determined. The Shasta snow-wreath occurrence points were then intersected with the digital Order 3 soil survey of the area (USDA Forest Service 1983), and the distribution of Shasta snow-wreath occurrences by Order 3 soil map unit was determined.

Each new population was also field-checked for evidence of unmapped limestone outcrops, since there are occasional exposed limestone inclusions within the Shasta Lake area that are too small to be included in landscape-scale geology or soil maps.

Results

Nine of the 17 known Shasta snow-wreath occurrences intersected the mapped extent of limestone bedrock and are found within limestone geologic types (Table 1). The remaining eight occurrences are found within primarily metavolcanic and metasedimentary geologic types.

Three of the 17 known Shasta snow-wreath occurrences intersected the mapped extent of Order 3 soil map units with limestone parent material (Table 2). However, six additional occurrences are located immediately adjacent to, or downstream of limestone outcrops; where there is a high likelihood that colluvial or fluvially transported limestone substrate is present; or are located within limestone inclusions occurring within the Order 3 soil mapping unit. Collectively, nine Shasta snow-wreath occurrences are either located within, or are immediately adjacent to soil types containing limestone parent material. The remaining eight occurrences are found within primarily metasedimentary/metavolcanic Order 3 soil map units.

Discussion

Of our seven new Shasta snow-wreath discovery locations, only one intersected the mapped

TABLE 1. DISTRIBUTION OF *NEVIUSIA CLIFTONII* OCCURRENCES BY GEOLOGIC TYPE.[1]–Also contains limestone fragments and strata.

Geologic map unit	Formation	Rock type	Age	No. Shasta snow-wreath occurences
Cb	Baird	Metasedimentary	Carboniferous	2
Cbmv	Baird	Metavolcanic	Carboniferous	1
Dc	Copley Greenstone	Metavolcanic	Devonian	1
Pmd	Quartz Diorite – Dikes	Intrusive	Permian	1
Pmml	McCloud Limestone	Carbonaceous	Permian	1
Pmn	Nosoni	Metasedimentary/ metavolcanic	Permian	1
Trh	Hosselkus Limestone	Carbonaceous	Triassic	4
Trm	Modin	Metavolcanic[1]	Triassic	3
Trp	Pit	Metasedimentary	Triassic	3

TABLE 2. DISTRIBUTION OF *NEVIUSIA CLIFTONII* OCCURRENCES BY ORDER 3 SOIL TYPE.

Order 3 soil map unit	Dominant soil type	Dominant parent material	No. Shasta snow-wreath occurrences
102	Holland Family	Metasedimentary/metavolcanic	1
105	Holland Family	Metasedimentary/metavolcanic	5
117	Holland Family, deep	Metasedimentary/metavolcanic	1
178	Marpa Family	Metasedimentary/metavolcanic	1
179	Marpa Family	Metasedimentary/metavolcanic	1
180	Marpa Family	Metasedimentary/metavolcanic	1
183	Marpa Family	Metasedimentary/metavolcanic	1
195	Millsholm Family	Sedimentary	1
204	Neuns Family	Metasedimentary/metavolcanic	1
222	Neuns Family	Metasedimentary/metavolcanic	1
250	Rock Outcrop, limestone	Limestone	3

extent of limestone bedrock. With the addition of these seven new sites, there are now seventeen documented Shasta snow-wreath occurrences. Following our GIS analysis of the geologic and soil characteristics at each location, nine of the 17 Shasta snow-wreath occurrences intersect the mapped extent of limestone bedrock, or occur immediately adjacent to or downstream of limestone outcrops. The remaining eight locations, including four of the five most extensive populations, are found in non-limestone habitats.

These seven new Shasta snow-wreath discoveries have nearly doubled the number of known occurrences. Additionally, the geology and soil type analysis of these locations show that nearly one-half (47%) of the known species locations occur in habitats not associated with limestone rock formations nor soils formed from limestone parent material.

Though these new occurrences have filled some gaps in the known distribution, they are within the previously recorded species range. Most of the documented Shasta snow-wreath occurrences are located within the eastern half of the Shasta Lake region in the Pit River, Squaw Creek, and McCloud River drainages. One occurrence lies within the western half of the Shasta Lake region in the Sacramento River drainage. Given our analysis of the geologic and edaphic characteristics at the known Shasta snow-wreath sites, the previous assumptions regarding the species geologic and edaphic associations, and the fairly limited geographic extent of previous survey efforts, only a small fraction of potential habitat for this species has been surveyed, and it is highly likely that additional populations occur.

The conservation implications from these new Shasta snow-wreath discoveries may be described as two-fold. These new populations, in terms of both numbers of known occurrences and more widespread geologic/edaphic associations, show that the species may not be as rare or narrowly distributed as initially thought. However, six of the known populations have already been at least partially flooded by the creation of Shasta Lake. Additionally, these new discoveries also show that the species is still likely a narrow endemic to the Shasta Lake region. Endemism within this region is already fairly well documented by the presence of several endemic plant and wildlife species including Shasta eupatory (*Ageratina shastensis*), Shasta salamander (*Hydromantes shastae*), Shasta sideband snail (*Monadenia troglodytes troglodytes*), and Wintu sideband snail (*M.t. wintu*), and is likely a function of geologic and climatic factors. The geology of this region is considered ancient, particularly relative to surrounding regions, and was not affected by

glaciation, nor was overlain by volcanic material. Additionally, this region lies within an area of high annual precipitation at relatively low elevations, producing a combination of mesic conditions and mild temperatures. These geologic and climatic factors in the Shasta Lake region result in conditions favorable for a diverse flora and fauna, including several endemic species.

The boundaries of Shasta snow-wreath's geographic and elevational range have yet to be determined. It is clear from our analysis of geologic and edaphic characteristics at the known snow-wreath population sites that non-limestone substrates cannot be excluded as suitable habitat, and that field inventories for Shasta snow-wreath within the species known distribution should include a wider range of substrates, aspects, and vegetation types than was thought suitable for the species.

Acknowledgements

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ADDITIONAL TAXONOMIC STUDIES OF *ARCEUTHOBIUM PENDENS* (VISCACEAE): A RARE DWARF MISTLETOE FROM CENTRAL MEXICO

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ABSTRACT

Additional measurements of male and female plants and staminate flowers are reported for *Arceuthobium pendens*. Measurements for fruits and seeds of this rare mistletoe are reported for the first time. Additional information on phenology and host reactions to infection is reported also.

RESUMEN

Se reportan mediciones adicionales de plantas masculinas y femeninas y de flores masculinas de *Arceuthobium pendens*. Las mediciones de frutos y semillas de esta rara especie de muérdago enano son reportadas por primera vez. Información adicional sobre fluoración y dispersión de semillas y reacciones del hospedero a la infección son también reportadas.

Key Words: pendent dwarf mistletoe, *Arceuthobium pendens*, *Pinus cembroides* subsp. *orizabensis*, *Pinus discolor*.

Arceuthobium pendens Hawksworth & Wiens (Viscaceae) was described in 1980 from the Sierra San Miguelito in southwestern San Luis Potosi, Mexico (Hawksworth and Wiens 1980). This dwarf mistletoe has only been discovered in two additional populations much farther south in Mexico and in close proximity to each other: northwest of Perote near Frijol Colorado in western Vera Cruz and on Cerro Pizarro in northeastern Puebla (Chazaro and Olivia 1987; Hawksworth and Wiens 1996; Hawksworth et al. 2002). Because this dwarf mistletoe is only known from three populations, it is currently considered to be one of the rarest dwarf mistletoes in Mexico (Hawksworth and Wiens 1996).

For this species, information on several morphological, phenological, and other attributes are limited or unavailable. When Hawksworth and Wiens (1980) described *Arceuthobium pendens*, they provided morphological data on the size and color of male and female plants and the size of staminate flowers. Because Hawksworth and Wiens' original specimens collected in 1979 from San Luis Potosi, as well as specimens collected by D. K. Bailey and T. Wendt in 1980 from Vera Cruz, were collected in early March, Hawksworth and Wiens did not have specimens of male plants with open flowers or female plants with mature fruits and seeds (Hawksworth and Wiens 1980). However, they were able to obtain measurements of staminate flowers from specimens collected by M. F. Robert in September 1971 that had male plants with mature staminate flowers. Hence, they concluded that *A. pendens* probably flowered in September, but acknowledged that this was only an estimate based on the Robert specimens. Information on the period of seed dispersal for *A. pendens* reported by Hawksworth and Wiens (1996) was based on a report by Chazaro and Olivia (1987) who first reported the occurrence of *A. pendens* in Puebla (Cerro Pizarro) and indicated that it dispersed seed from June to September.

Because of the small amount of data provided by Hawksworth and Wiens (1980, 1996) we collected many additional specimens of *A. pendens* from near Frijol Colorado in Vera Cruz in late July 2005. This allowed us to complete many additional measurements of male and female plants. Since many male plants had begun flowering and several female plants had started seed dispersal, we were also able to measure male flowers and collect the first data on the size of mature fruits and seeds as well as estimate the periods of peak seed dispersal and flowering for *A. pendens* in Vera Cruz. These additional and new morphological measurements allowed us to make further comparisons between *A. pendens* and *A. divaricatum* Engelm., the only other dwarf mistletoe that parasitizes pinyons as principal hosts.

A total of 60 infected branches with plants of *A. pendens* (30 males and 30 females) were collected from 30 severely infected *Pinus orizabensis* trees approximately 8 km north of Frijol Colorado along the road to Los Humeros in western Vera Cruz, Mexico (19°37′N, 97°23′W, elev. 2740 m).

One male and one female infection with mature plants were collected from the lower part of the crown of each tree. Infections were collected haphazardly in that the first observed and easily accessed male and female infection with mature plants was sampled. The approximate location of this population is illustrated in Fig. 16.85 of Hawksworth and Wiens (1996). The plants were placed in paper bags, and all measurements were made within 24 hr of collection. The dwarf mistletoe plant characters measured were primarily those used by Hawksworth and Wiens (1996) in their monograph of *Arceuthobium*. The following morphological characters were recorded: 1) height and color of the tallest male and female plant from each infection collected; 2) mature fruit length, width, and color; 3) seed length, width, and color; 4) staminate flower diameter; 5) number, length, and width of staminate perianth lobes; 6) anther distance from the perianth lobe tip; 7) anther diameter; and 8) pre-flowering lateral staminate spike length and width. Dwarf mistletoe plants were measured using a Plasti-cal digital caliper accurate to 0.1 cm and all other measurements were made with a Bausch and Lomb 7× hand lens equipped with a micrometer accurate to 0.1 mm.

Specimens of male and female plants of *A. pendens* collected from the Vera Cruz population have been deposited at the Deaver Herbarium (ASC), Northern Arizona University, Flagstaff, AZ.

The heights of male and female plants (Table 1) were much greater than those reported by Hawksworth and Wiens (1980, 1996) for plants of *A. pendens* collected in the Sierra San Miguelito of San Luis Potosi. Hawksworth and Wiens (1980, 1996) reported that the maximum plant size for male plants of *A. pendens* was 22 cm, but we measured male plants 32 cm in height and many male plants (30%) were greater than 25 cm in height. Furthermore, while Hawksworth and Wiens (1996) commented that few female plants of *A. pendens* were larger than 8 cm, we commonly found female plants (50%) greater than 15 cm in height and the tallest female plant we measured was 26 cm. While male and female plants were both predominantly light green, the base of several older plants was dark green, and for some of the largest male and female plants, the base was dark brown, indicating that as the plants age their bases gradually change color.

Although Hawksworth and Wiens (1980) did not report how many plants of each sex they measured, they did comment that they only found two infected pinyons at the Sierra San Miguelito type locality in San Luis Potosi. Therefore, they may not have been able to measure many plants from that location. Because many trees were infected at the Vera Cruz location, we were able to measure a fairly large sample of male and female plants. Therefore, our measurements are probably more representative of the mean sizes and ranges for male and female plants of *A. pendens*. Additional morphological measurements should be completed from the third population from Cerro Pizarro in Puebla to see how they compare to the Vera Cruz and San Luis Potosi populations.

The mean diameter of male flowers we obtained (2.6 mm) (Table 1) is approximately the same as that reported by Hawksworth and Wiens (2.5 mm). Most male flowers were 3-merous, but rarely 4-merous staminate flowers were observed on the terminal ends of staminate spikes.

Our measurements for perianth lobes, anthers, and staminate spikes, mature fruits and seeds (Table 1) are the first reported for *A. pendens*.

Most fruits were the same color as female plants, but some female plants had fruits that were dark green while the plants were light green. Seeds were light green and lacked the characteristic yellow cap that many species of *Arceuthobium* have on their mature seeds (Hawksworth and Wiens 1996).

Because several male plants had started flowering and several others had most of their flowers open in late July, it appears that the flowering period for *A. pendens* is probably from early July–September. Based on these observations, the peak flowering period is probably in August in Puebla and Vera Cruz and not in September as estimated for the San Luis Potosi population by Hawksworth and Wiens (1980).

Seed dispersal had already started for several female plants in late July and some female plants had nearly completed seed dispersal. Therefore, the seed dispersal period reported by Chazaro and Olivia (1987) of June–September is a good approximation. However, because many female plants had immature fruits in late July in the Vera Cruz population, the seed dispersal period may extend into early October for this population.

Typically, infections by *A. pendens* were non-systemic and did not induce witches' brooms, but when brooms were formed on trees in Vera Cruz, they were always associated with systemic infections as reported by Hawksworth and Wiens (1980, 1996) for the San Luis Potosi population. We observed that the systemic witches' brooms formed on some infected trees were induced by both male and female plants, but most of these brooms were associated with male plants as reported by Hawksworth and Weins (1980, 1996); we only observed three systemic witches' brooms induced by female plants versus over 50 induced by male plants. In a few cases, systemic witches' brooms induced by male plants had one or even two female plants infecting one of the systemically male-infected branches within the broom. We did not see any female-induced systemic witches' brooms with male plants, but this condition probably occurs as well.

TABLE 1. MORPHOLOGICAL CHARACTERS MEASURED FOR 30 MALE AND 30 FEMALE PLANTS (PLANT HEIGHTS) AND FOR 50 STAMINATE FLOWERS, FRUITS, AND SEEDS OF *ARCEUTHOBIUM PENDENS* FROM VERA CRUZ, MEXICO.

Character	Mean	Standard Deviation	Range
Mean Plant Height (cm)			
Male	23	4.9	16–32
Female	16	4.2	7–26
Staminate Flower Diameter (mm)	2.6	0.1	2.3–2.9
Perianth Lobe Length (mm)	1.2	0.1	1.0–1.3
Perianth Lobe Width (mm)	1.1	0.1	0.9–1.2
Anther Diameter (mm)	0.6	0.1	0.5–0.8
Distance of Anther From Tip of Perianth Lobe (mm)	0.4	0.1	0.2–0.6
Staminate Spike Length (mm)	8	2.5	3–13
Staminate Spike Width (mm)	0.9	0.1	0.8–1.1
Fruit Length (mm)	3.4	0.4	2.6–4.1
Fruit Width (mm)	1.8	0.2	1.4–2.2
Seed Length (mm)	2.3	0.2	1.9–2.7
Seed Width (mm)	0.9	0.1	0.7–1.1

The mean diameter of staminate flowers and the mean length and width of fruits and seeds for *A. pendens* are approximately the same as those reported for *A. divaricatum*, the other dwarf mistletoe that parasitizes pinyons as principal hosts (Hawksworth and Wiens 1996). Although the size of male flowers, fruits, and seeds are similar for these two dwarf mistletoes, the morphology of the male and female plants is different for these taxa. Male and female plants of *A. pendens* are much larger (means 23 and 16 cm, respectively; maximum plant height 32 cm), than *A. divaricatum* (mean for all plants 8 cm; maximum height 13 cm) (Hawksworth and Wiens 1996). In addition, the light green color of male and female plants of *A. pendens* is in marked contrast to the dark greenish-brown plants of *A. divaricatum*. The male plants of *A. pendens* are commonly pendent as reported by Hawksworth and Wiens (1980), which is a clear contrast to the habit of male plants of *A. divaricatum* (Hawksworth and Wiens 1996). Furthermore, the flavonoid chemistry of *A. pendens* and *A. divaricatum* is quite different (Hawksworth and Wiens 1980) and the molecular evidence strongly supports the segregation of these dwarf mistletoes as separate species (Nickrent et al. 2004).

Although Hawksworth and Wiens (1980) initially classified the host of *A. pendens* in Vera Cruz as *P. cembroides* Zuccarini, they later classified this pinyon population as *P. orizabensis* (Hawksworth and Wiens 1996; Hawksworth et al. 2002) based on a taxonomic treatment of this pinyon population proposed by Bailey and Hawksworth (1992). In San Luis Potosi, *A. pendens* was not observed parasitizing *Pinus cembroides*, although trees of this species were observed in the vicinity of the infected *Pinus discolor* D. K. Bailey & Hawksworth observed there (Hawksworth and Wiens 1980). While Hawksworth and Wiens (1996) and Hawksworth et al. (2002) have classified the host of *Arceuthobium pendens* at the Vera Cruz and Puebla locations as *Pinus orizabensis*, monographs of *Pinus* for Mexico and Central America by Perry (1991) and Farjon and Styles (1997) classify these pinyon populations as *P. cembroides* subsp. *orizabensis* D. K. Bailey. Whether or not *A. pendens* infects *P. cembroides* further north in Mexico needs to be determined and further research on the host range of *A. pendens* is definitely needed in central Mexico. However, finding additional populations of this cryptic and probably very rare dwarf mistletoe may prove difficult as suggested by Hawksworth and Wiens (1980).

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A NEW SPECIES OF SILENE IN THE *SILENE HOOKERI* COMPLEX (CARYOPHYLLACEAE) FROM THE KLAMATH MOUNTAINS OF SHASTA-TRINITY NATIONAL FOREST, TRINITY COUNTY, CALIFORNIA

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ABSTRACT

Silene salmonacea T.W. Nelson, J. P. Nelson and S.A. Erwin is here described as new and illustrated; endemic to the Klamath Mountains of Shasta -Trinity National Forest west of Clair Engle Lake. *Silene salmonacea* is compared with *Silene hookeri* Nutt. and *Silene bolanderi* A. Gray. A key to the three members of the *S. hookeri* complex is included.

Key Words: *Silene*, serpentine, Trinity County, Weaverville Formation, Shasta-Trinity National Forest, Clair Engle Lake, California.

DESCRIPTION

Silene salmonacea T.W. Nelson, J. P. Nelson and S. A. Erwin, sp. nov. (Figs. 1–3). Perennes; rhizomata tenuia ramose. Ad radicem palarem profundam affixa; caules erecti 5–14 mm longi canescentes; folia congesta, paribus 3–4, spathulati-oblanceolata, 25–35 mm longa, 4–6 (–8) mm lata; inflorescentia terminalis floribus 2–3 (–4); calyx distincte 10 nervatis; corolla limbo salmonaceo in lobos 4 fere equales diviso, unguis viridis basi albus; appendices petaloideae virides vel albae, lineares, 2 in quoque petalo, 1.8–2 mm longae 0.5–1 mm latae; antherae longiexertae; stylus inclusa.

Perennial; stems 5–14 mm long; erect from thin branching rhizome system arising from deep, thickened tap root, gray-green, canescent; cauline leaves 3–4 pairs, crowded, spathulate to oblanceolate, 25–35 mm long, 4–6 (–8) mm wide, gray-green, the lowest much reduced in size; inflorescence terminal, 2–3 (–4) flowered; calyx gray-green, canescent, distinctly 10 nerved, 18–23 mm long, teeth ciliate, lanceolate, 4–7 mm long, expanding in fruit; limb of corolla salmon-orange colored (Fig. 3), palmately partite into 4 nearly equal obtuse lobes, the lobes 8–10 mm long, inner 2 lobes 2.4–2.5 mm wide, the outer 2 lobes 1.75–2 mm wide, the limb considerably wider than claw; claw glabrous, green becoming white at base; petal appendages 2, linear, 1.8–2 mm long, 0.5–1.0 mm wide, light green to white, contrasting with salmon colored limb; filaments 16–17 mm long, long exerted; styles 3, ca. 9 mm long, included; ovary 4 mm long, green; seeds reniform, reddish-brown, 2.18 × 1.5 mm, strongly papillate, the papillae in parallel rows (Fig. 2).

Type: USA, CA, Trinity County, T36N R8W sect. 22 SE ¼ NW ¼. UTM 4534856N 0519803E. Elev. 1043 m (3421 ft). Shasta-Trinity National Forest. NW of Forest Service Road 36N25 (County Road 123) ca. ¼ mile NW from bridge over Cement Creek. Serpentine hillside recently disturbed by logging. 3 June 2004. *T. W. Nelson & S. A. Erwin 9218* (HOLOTYPE: HSC; Isotypes: CAS, RM, UC, MO, MICH.)

Paratypes: USA, CA, Trinity County: T36N R8W sect. 22 SE ¼ NE ¼. Elev. 1020 m (3400 ft). About 400 m NW of crossing of Cement Creek by Forest Service Rd. 36N25. 4 June 2002. *D W. Taylor 18097*, (HSC); Haylock Ridge above Smith Gulch, Trinity Lake, T34N R9W sects. 1 & 12. 11 June 1978. *S. Horner s.n.* (Shasta-Trinity National Forest Herbarium); T34N R9W sect. 12. UTM 45128106N 0514653E. Elev. 774 m (2580 ft). Along Forest Service Road 34N80 between roads 34N73 & 34N71. Open areas in mixed evergreen forest and road banks. 8 June 2005. *T. W. Nelson & S. A. Erwin 9342* (HSC); T34N R4W sect. 6. UTM 4519536N 0514929E. Elev. 845 m (2815 ft). Along Forest Service Road 34N80 in opening in mixed evergreen woodland. 8 June 2005. *T. W. Nelson & S. A. Erwin 9345* (HSC). Duplicates are to be distributed.

Susan Erwin found two more populations each with less than five plants; so no collections were made. The locations are: Trinity County, west of Clair Engle Lake on the iron rich soil of the Weaverville Formation. T34N R8W sect. 19. Elev. 900 m (2952 ft) at the junction of roads 34N94 & 34N17Y and the other at T34N R9W sect. 9. Elev. 930 m (3650 ft) along road 113.

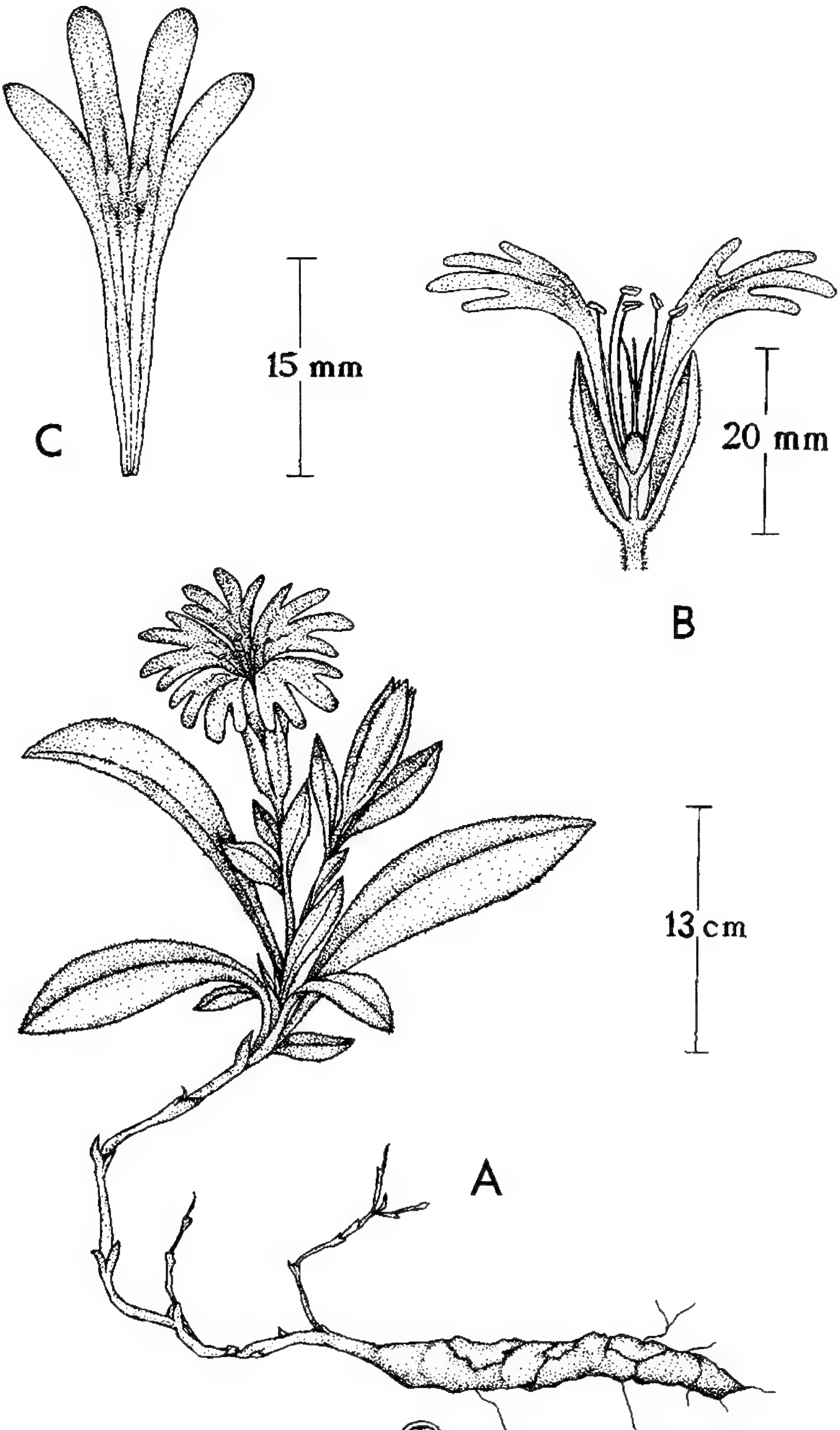

FIG. 1. Illustration of *Silene salmonacea*; A. Mature plant at anthesis. B. Flower in longitudinal section. C. Petal showing appendages.

FIG. 2. Photograph of the seeds of *Silene salmonacea*. Seeds are approximately 2 mm in length.

Silene salmonacea appears to be very rare, as it is only known from the type locality and five other sites. The populations range in number from 3 to 250 plants. It has been found on serpentine soils and the iron rich soils of the Weaverville Formation of the low hills of the Klamath Mountains west of Clair Engle Lake, where it occurs on either open serpentine or openings in mixed evergreen forests at elevations from 845 to 1043 m.

Incomplete descriptions (often based on a single specimen) have added some confusion to the treatment to the *Silene hookeri* complex. Nuttall (1838) described *Silene hookeri* based on a single specimen collected by Dr. Gardiner, and no type or lectotype has ever been designated. Gray (1868) named *S. bolanderi* but with no mention of its lack of petal appendages. Tidestrom and Dayton (1929) described *S. ingrami* based on a single incomplete specimen. They also failed to describe any petal appendages. Peck (1932) described *S. pulverulenta* based on a single incomplete specimen. His prolog was mostly written in Latin with only a brief commentary in English that included no comments about the petal appendages.

Subsequent to these species descriptions, Abrams (1944) reduced *S. bolanderi* to a subsp. of *S. hookeri* and *S. ingrami* and *S. pulverulenta* to synonyms of subsp. *hookeri*. In their revision of *Silene*, Hitchcock and Maguire (1947) recognized three subsps. of *S. hookeri*: subsps. *hookeri*, *bolanderi* and *pulverulenta*. Munz and Keck (1959) and Morton (2005) recognized only subsps. *hookeri* and *bolanderi*. Wilken (1993) only recognized a highly variable *S. hookeri*.

During our studies of the *S. hookeri* complex, we concluded that based on the different characters shown in Table 1, *S. bolanderi* should be recognized as a separate species rather than a subspecies of *S. hookeri*. Thus we consider, the *S. hookeri* complex to consist of *S. hookeri*, *S. bolanderi* and *S. salmonacea*. This is also the concept being followed by Hartman (personal communication) in his forthcoming revision for the Jepson Manual.

These three taxa of the *S. hookeri* complex are easily distinguished. *Silene bolanderi* is separated from the other two because it lacks petal appendages and is the only member with white flowers. In addition to differences in petal color, *S. hookeri* can be easily separated from *S. salmonacea* by the fact that the anthers are included while those of *S. salmonacea* are long exerted. Additional details are included in Table 1.

FIG. 3. Photograph of *Silene salmonacea* at type locality.

A KEY TO THE CALIFORNIA *SILENE HOOKERI* COMPLEX

A. Petal appendages absent; limbs white or tinted green . . . . *Silene bolanderi*

A′ Petal appendages 2; limbs pink or salmon-orange

B. Anthers included, petal lobes either 2 each with a small lateral tooth or 4 and unequal; limb and claw pink adaxially, white abaxially . . . . *Silene hookeri*

B′ Anthers excluded, petals with 4 nearly equal parallel lobes; limbs salmon-orange, claws white becoming green at base . . . . *Silene salmonacea*

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TABLE 1. MORPHOLOGICAL COMPARISON OF SPECIES IN THE *SILENE HOOKERI* COMPLEX.

	Silene salmonacea	*Silene bolanderi*	*Silene hookeri*
Petal colors	Limb salmon-orange, Claw white becoming green at base	Limb and claw both white tinted green	Limb and claw pink adaxially, white abaxially
Lobes of limb	4, equally palmately dissected nearly to base, tip obtuse	4, equally palmately dissected nearly to base, tip acute	2 lobes each with a small lateral tooth or 4 unequal lobes
Petal appendages	2	0	2
Stems	1–2, reclining to erect from thin rhizomes	1–3, erect from thin rhizomes	3–5, reclining from root crown
Anthers	Long exerted	Long exerted	Included

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LEPECHINIA ROSSII (LAMIACEAE), A NARROW ENDEMIC FROM THE WESTERN TRANSVERSE RANGES OF SOUTHERN CALIFORNIA

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ABSTRACT

Lepechinia rossii (Lamiaceae) is described as a new species narrowly endemic to the western Transverse Ranges of southern California. It is a member of section *Calycinae*, which includes four additional species endemic to California and adjacent Baja California, Mexico—*L. calycina, L. cardiophylla, L. fragrans, L. ganderi*—and *L. mexicana*, an anomalous, and probably unrelated, species from central Mexico. *Lepechinia rossii* is most readily distinguished from other members of section *Calycinae* by geniculate inflorescence axes, bent at 60–90° angles relative to the subtending stems, and by large, foliaceous inflorescence bracts which are generally equaling or exceeding their adjacent flowers in length, and little reduced distally. At present, two populations are documented, one in the Liebre Mountains (Los Angeles County) and one in the Topatopa Mountains (Ventura County), both occurring in chaparral, on public lands administered by the U.S. Forest Service. Conservation concerns include habitat degradation by off-highway vehicle activity, power line maintenance, petroleum exploration and extraction, and anthropogenic changes in fire frequency.

RESUMEN

Lepechinia rossii (Lamiaceae) es descrita como una nueva especie con endemismo limitado a la cadena Transverse Ranges (occidental) del Sur de California. Esta especie es un miembro de la sección *Calycinae*, la cual incluye cuatro especies adicionales endémicas a California y zonas adyacentes a California en Baja California, Mexico—*L. calycina, L. cardiophylla, L. fragrans, L. ganderi*—y *L. mexicana*, anómalos y probablemente no relacionadas, especies de Mexico central y sur-central. *Lepechinia rossii* es facilmente diferenciado de los otros miembros de la sección *Calycinae* porque sus ejes de la inflorescencia son curvados en un ángulo de 60–90° con respecto al tallo y porque las brácteas de la inflorescencia son largas y foliaceas, las cuales son generalmente iguales o exceden en longitud a sus flores adyacentes y porque el tamaño de las brácteas a lo largo del eje de la inflorescencia apenas se reduce en longitud. En la actualidad, dos poblaciones son documentadas, una en la Liebre Mountains (Condado de Los Angeles) y la otra en la Topatopa Mountains (Condado de Ventura), ambas se encuentran en chaparrales, sobre terrenos publicos administrados por el Servicio Forestal de los Estados Unidos. Problemas de conservación incluye degradación del habitat por actividad todoterrenos, mantenimiento de lineas de electricidad, exploración y extracción de petroleo, y cambios antropogénicos en la frecuencia de incendios.

Key Words: California, *Calycinae*, endemic, Lamiaceae, *Lepechinia*, Liebre Mountains, Topatopa Mountains, Transverse Ranges.

INTRODUCTION

Lepechinia Willd. (Lamiaceae) is a heterogenous genus comprised of ca. 55 species of suffruticose perennials, shrubs, and small trees (Epling 1948; Mabberly 1997). Most taxa occur in the mountains of South America, with a few species extending into North America (Mexico, CA), and disjunctly, into the Pacific Ocean archipelagos of Revillagigedos (Mexico) and Hawai'i (Epling 1948). The most recent broad-scale floristic treatments for California (e.g., Munz 1959; Averett 1993), and southern California (Munz 1974), recognize four species of *Lepechinia* in the State. These include *L. calycina* (Benth.) Epling; *L. cardiophylla* Epling; *L. fragrans* (E. Greene) Epling; and *L. ganderi* Epling. The latter three taxa are found only in the southern third of the State, from the Transverse Ranges and northern Channel Islands southward, with two (*L. cardiophylla*, *L. ganderi*) reaching adjacent northwestern Baja California, Mexico (Fig. 1A). All four taxa are placed by Epling (1948) within his section *Calycinae*, along with *L. mexicana* (S. Schauer) Epling from central Mexico. We describe here a fifth species of *Lepechinia* section *Calycinae* from California—*Lepechinia rossii* S. Boyd & O. Mistretta—based on collections made in the Liebre and Topatopa mountains, two units of southern California's western Transverse Ranges. Although the affinity of *L. rossii* with other Californian members of *Lepechinia* section *Calycinae* is evident in a number of variously shared morphological characters (e.g., habit, leaf shape, leaf vestiture, calyx shape, corolla size and shape)—Epling's "living mosaic" (1944)—it is a suite of inflorescence characters that most

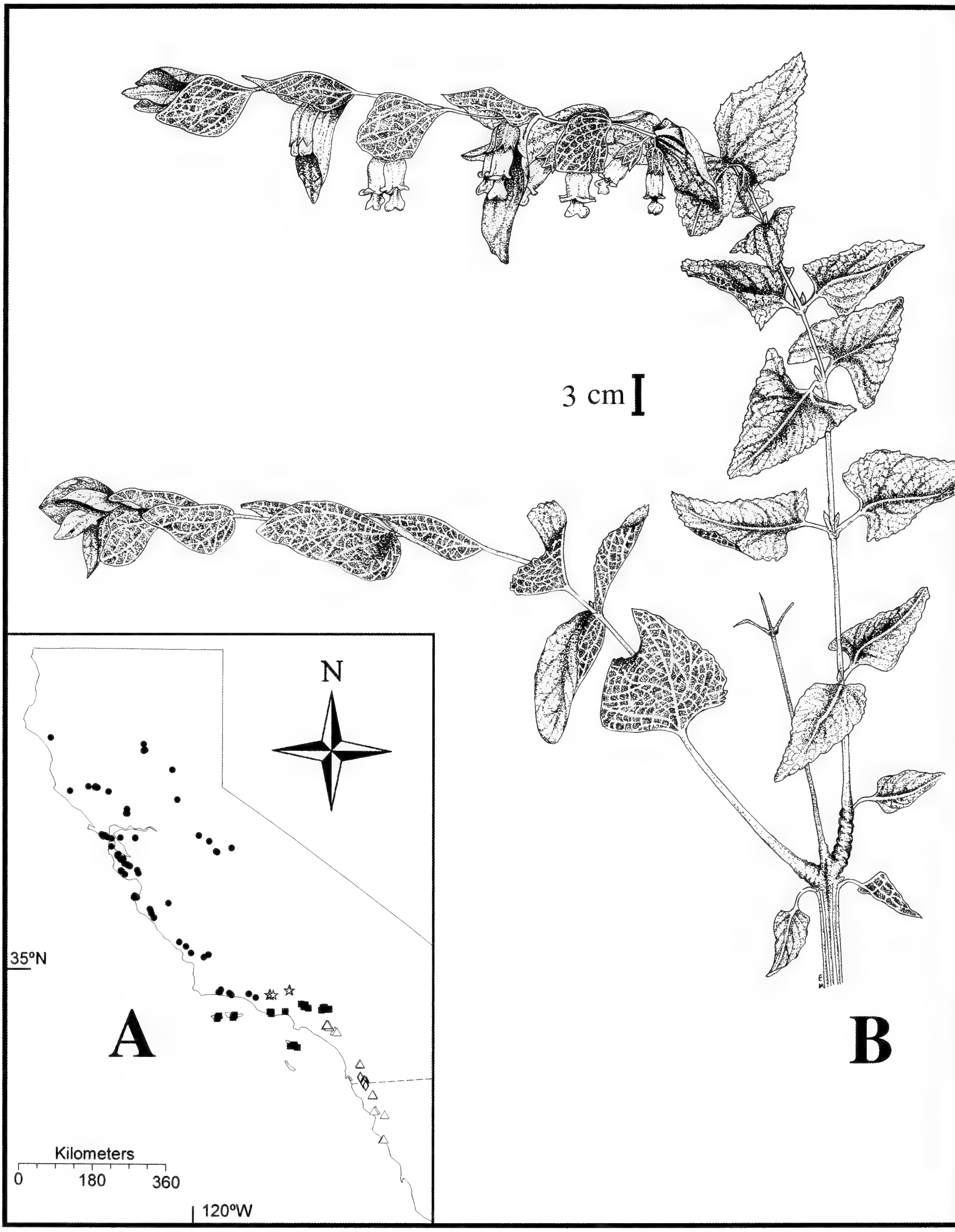

FIG. 1. *Lepechinia rossii*. A) map showing relative distribution of *Lepechinia* sect. *Calycinae* taxa in California and northern Baja California, Mexico. *Lepechinia rossii*—open stars; *L. calycina*—closed circles; *L. fragrans*—closed squares; *L. cardiophylla*—open triangles; *L. ganderi*—open diamonds. B) illustration of portion of an upper stem bearing two inflorescences, showing typical leaves, bent primary inflorescence axes, broadly ovate to suborbicular, overlapping floral bracts, and pendant flowers.

readily set *L. rossii* apart from all other members of the genus. These include orientation of the inflorescence axes, size, shape, and orientation of the floral bracts, and the degree to which these bracts are reduced apically.

Although two non-flowering, historical specimens of *Lepechinia* from the Topatopa Mountains, B.W. Evermann (Pine Creek near Sespe; 24 Mar 1917 [CAS #25345]), or R. Hoffmann (Sespe Canyon; 21 Mar 1927 [SBBG #6403; #6404]), are likely the earliest collections of this plant, from a practical standpoint *L. rossii* was "discovered" in the Fall of 1991. While conducting botanical surveys for the Angeles National Forest in late September of that year, the second author collected a sterile, partially deciduous *Lepechinia* on Red Mountain, between San Francisquito and Elizabeth Lake canyons, in the Liebre Mountains region of northwestern Los Angeles County. Upon seeing this specimen, Timothy S. Ross, then a senior curatorial assistant in the herbarium at Rancho Santa Ana Botanic Garden (RSA), immediately noted that *Lepechinia* was otherwise unknown in the Liebre Mountains, and the find was therefore of interest from a floristic standpoint. At the time, Ross speculated Mistretta's plant was likely *L. fragrans*, as that species is found in the San Gabriel and Santa Monica mountains, regions of the Transverse Ranges lying to the southeast and southwest of the Liebre Mountains, respectively.

In the spring of 1992, Ross and the first author visited the Red Mountain area and found a population of *Lepechinia* growing on the mountain's northern slope and upper ridgelines (ca. 500–1000 individuals). So distinctive were the plants in flower (geniculate inflorescence axes, with large, foliaceous, upwardly directed floral bracts, little reduced apically and generally longer than their adjacent flower) that it was instantly clear they were not *L. fragrans*, nor did they appear to fit any of the other Californian taxa in the genus. In Fall of 1995, while examining *Lepechinia* specimens from Santa Barbara Botanic Garden (SBBG), Ross encountered an E.R. Blakley collection from Tar Creek in the Topatopa Mountains (Ventura County; Los Padres National Forest), collected in 1994, that appeared consistent with the undescribed taxon from Red Mountain. Ross and the authors visited Blakley's Tar Creek site in Spring of 1995 and confirmed the Topatopa Mountains plants were the same undescribed entity as those of the Liebre Mountains. The Tar Creek site is ca. 40 km west of Red Mountain, and as a tributary of Sespe Canyon, in the general vicinity of the sterile 1917 and 1927 collections mentioned above.

In light of the central role our friend and colleague, Timothy S. Ross has played in the discovery and understanding of this new *Lepechinia*, it is our pleasure to name this species in his honor. For the vernacular, we recommend the plant be called Ross' pitcher sage.

Description

Lepechinia rossii S. Boyd & O. Mistretta, sp. nov. (Fig. 1B)—Type: USA, California, Los Angeles Co., Transverse Ranges, Liebre Mountains region: Head of Ruby Canyon on northern flank of Red Mountain, between Elizabeth Lake and San Francisquito canyons; 34°35′33″N, 118°29′29″W [NAD 27]; 305 m (1000 ft); 11 May 2004, *S. Boyd & T. Morgan 11169* (holotype RSA; isotypes CAS, GH, SBBG, UC, UCR, US). Paratypes: USA, California, Los Angeles Co., Transverse Ranges; San Gabriel Mtns region: Red Mountain [*technically* Liebre Mountains]; 25 Sep 1991, *O. Mistretta* s.n. (RSA). Transverse Ranges; Liebre Mountains region: Ruby-Clearwater Truck Trail, south of Ruby Canyon, north of Red Mountain; near 34.59788°N, 118.52618°W [NAD 83] (Warm Springs Mountain 7.5 quad); T6N R16W sect. 24, SW¼ of NE¼); 788 m (2585 ft); 24 May 2005, *L. Gross et al. 2311* (RSA). Ventura Co., Topa Topa [=Topatopa] Mountains, southern flank of Tar Creek, ca. 1 air mile southeast of confluence with Sespe Canyon, along an old dirt road leading down to Sespe Canyon off of Squaw Flat Road, about the base of hill "2582" at the boundary of the Sespe Condor Sanctuary; T5N R20W [sections] unsurveyed; ca. 732 m (2400 ft); 12 Jun 1996, *S. Boyd et al. 8849* (RSA). Tar Creek, on edge of old road down to Green Cabins on Sespe Creek; 549 m (1800 ft); 12 Jun 1994, *E.R. Blakley 7611* (SBBG).

Differt a *Lepechinia calycina, L. cardiophylla, L. fragrans*, et *L. ganderi* inflorescentia e basi 60–90° geniculatus et inflorescentiae bracteis foliaciis, plus minusve ultra flores.

Shrub, often forming clonal stands following disturbance or fire, generally less than 1.5 m tall with numerous ascending to erect branches from base and strongly aromatic herbage (Fig. 2); *stems* weak, ± brittle, those developing from short-shoots formed in upper axils of previous season's growth (vs. root or stem suckers) somewhat thickened towards base, with numerous, closely spaced leaf scars, growth of current season pale green, minutely glandular-puberulent with short-stipitate and subsessile capitate-glandular trichomes (appearing ± papillate at 20 × magnification), and scattered multicellular, clear, kinked, irregularly branched, nonglandular trichomes (to 1.5 mm long), older branches with bark becoming reddish brown and shredding in age; *leaves* opposite, with petioles ca. 5–20 (–30) mm long, often slightly winged distally, blades bright, light green or yellowish green, ovate to deltate-ovate, ca. 3–13 cm long, truncate to subcordate at base, margins irregularly and

FIG. 2. Type plant of *Lepechinia rossii* growing in relatively open area surrounded by chaparral vegetation, showing typical rounded crown, geniculate inflorescence axes, and prominent, ascending bracts.

shallowly serrulate to dentate, upper (adaxial) surface shallowly bullate, lower (abaxial) surface with prominent, raised, reticulate venation, vestiture as on stems, and with scattered, golden, sessile, hemispherical glands set in shallow pits (especially below); *inflorescence* terminal on growth of current season, geniculate, bent ± 60–90° relative to subtending stem and thus arching or spreading, axis shallowly curved between nodes, appearing scalloped (Figs. 1B, 2; 3A), unbranched, or more often with two short branches arising at lowest node, especially on vigorous stems; *bracts* foliaceous (Figs. 1B, 3B), sessile, ascending, broadly ovate to suborbicular, 2.5–8 cm, generally longer than subtended flower and not strongly reduced in size distally, therefore appearing imbricate towards apex of inflorescence, margins entire or the lowest 2–4 pairs shallowly serrulate to dentate, surfaces ± similar to leaves but less ruggose adaxially, raised veins of abaxial surface visually prominent, and long multicellular hairs sparse or absent; *flowers* solitary in bract axils, pendent on minutely glandular-puberulent pedicels 12–13 mm long (Figs. 3B, 4A); *calyx* at anthesis ± campanulate, the tube 10–12 mm long, finely raised-reticulate veined between 12–15 thicker longitudinal veins from base (Figs. 1B, 4B), minutely glandular-puberulent externally, ± glabrous internally, the lobes generally erect or slightly spreading, broadly deltate, 4–6 mm long × 4–6 mm wide, the apex abruptly short apiculate, frequently one or more lobes with single, apiculate, deltate marginal tooth 0.5–1.5 mm long × 0.5–1.5 mm wide, fruiting calyx enlarging, becoming somewhat inflated, papery; *corolla* overall broadly tubular (Figs. 1B, 3B, 4B), 33–39 mm long, abruptly narrowed in the proximal 8–9 mm, the point of narrowing marked internally by a ring of short, glandular hairs, broad portion of tube exerted from calyx ca. 15 mm, somewhat angled externally below point of stamen attachment, throat 10–11 mm wide, limb 5-lobed, strongly bilateral, the two lateral and two upper (adaxial) lobes short, 3.5–4.5 mm long × 4.5–6 mm wide, rounded apically, spreading to recurved, the lower (abaxial) lobe much larger, 10–12 mm long × 9–10 mm wide, deltate-ovate, erect, ± downfolded longitudinally forming a slightly raised palate, apex entire to slightly emarginate, tube and limb glandular-puberulent externally, initially pale yellowish cream with small maroon spots (especially abaxially), sometimes lobes and throat also flushed with pale pinkish maroon, base-color quickly fading to off-white after limb is fully expanded, spots and flush becoming very pale or disappearing; *anthers* included within corolla tube, didynamous, filaments glabrous, free portion of long pair 8–9 mm, of short pair 4.5–5 mm, anther sacs divergent, lobes ca. 2 mm long; *style* including stigma 20–21 mm long, pale pinkish, stigma bilobed, sometimes protruding from buds before limb is fully expanded; *nutlets* 4, 3–3.5 mm diam., ± spherical, glossy black, appearing glabrous at 20× magnification.

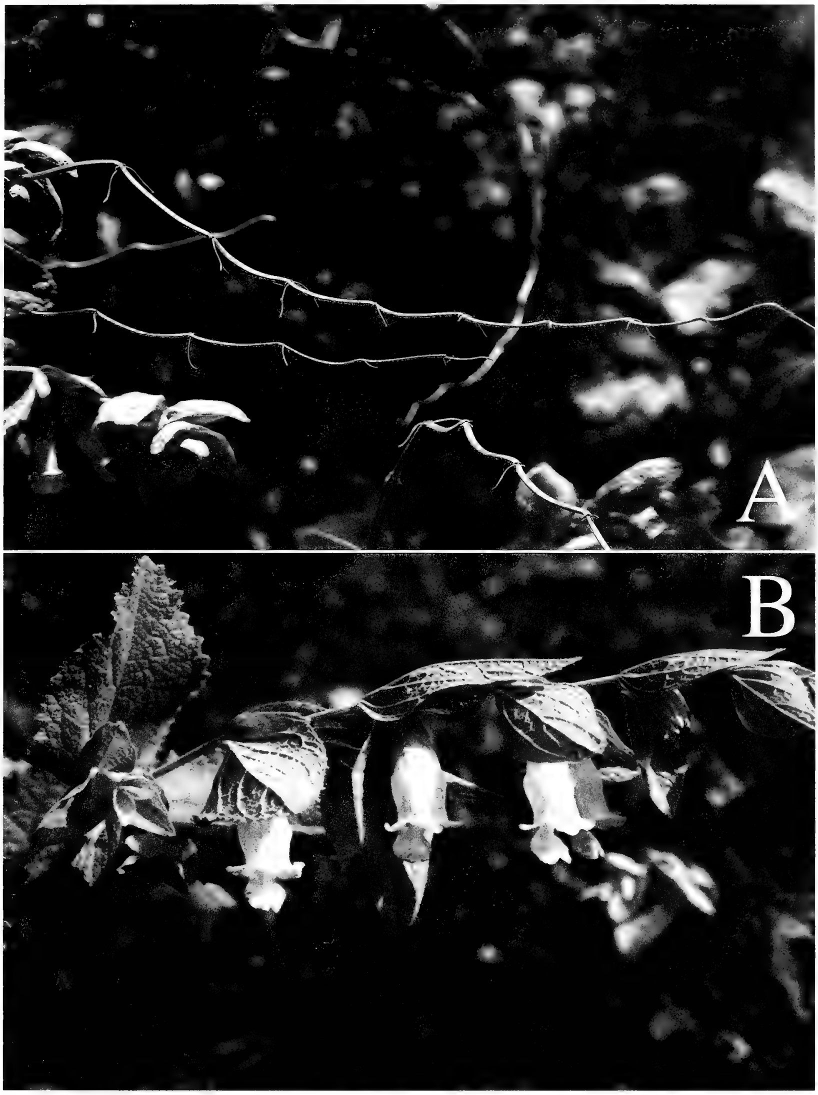

FIG. 3. *Lepechinia rossii*. A) detail of post-fruiting inflorescence axis showing shallow scalloping between nodes (marked by remnants of the pedicels). B) inflorescence at full anthesis showing relatively large foliaceous inflorescence bracts equaling or exceeding their adjacent flowers in length and only slightly reduced in size distally.

DISCUSSION

Relationships

As currently circumscribed, *Lepechinia* of California and northwestern Baja California, Mexico (*L. calycina, L. cardiophylla, L. fragrans*, and *L. ganderi*) are highly aromatic, weak-wooded shrubs (generally under 2 m tall), with deltate to oblong-ovate, drought-deciduous leaves, often subhastate or subcordate basally, and well developed, terminal inflorescences bearing relatively large, broadly tubular flowers that are solitary in axils of ± foliose bracts (Averett 1993). All four of these taxa are members of Epling's (1948) section *Calycinae*.

As originally circumscribed, section *Calycinae* contained five species, the four above, and a fifth, *L. mexicana* (S. Schauer) Epling, a small, woody shrub found in xeric regions of central and south-central Mexico, including the states of Hidalgo, Oaxaca, Puebla, and San Luis Potosi (Epling 1948). *Lepechinia rossii* becomes the sixth member of the section, and the fifth species of the genus in California.

Species relationships among members of *Lepechinia* section *Calycinae* are complex. *Lepechinia mexicana*, however, is quite anomalous, both geographically and morphologically, with respect to the other members of section *Calycinae*, including *L. rossii*, and does not appear to be closely related to the Californian taxa (T.S. Ross

FIG. 4. *Lepechinia rossii*. A) detail of relatively large foliaceous inflorescence bracts equaling or exceeding their adjacent flowers in length, and bilateral corolla with much enlarged lower lip. B) closer view of flower showing campanulate calyx with broadly deltate, short apiculate lobes, fine, raised, reticulate veins between prominent rib-like veins, and corolla tube that is somewhat angled externally above point of stamen insertion (lower lip of corolla is projecting straight out from plane of picture).

personal communication). In addition to the great range disjunction between *L. mexicana* and the five Californian species, the former differs in its herbage being densely grayish stellate-canescent, a type of pubescence not seen among the Californian members of the genus. The leaves of *L. mexicana* have revolute margins, and flowers are axillary along the stems, rather than being borne in terminal inflorescences subtended by highly modified bracts. The pedicels of *L. mexicana* bear two filiform bracts towards their base. The pedicels are bractless in the other five taxa. While it is likely *L. mexicana* is misplaced within section *Calycinae*, fully re-

solving that issue is beyond the scope of this paper. For the purposes of subsequent discussion, we have excluded *L. mexicana*.

Epling (1944) observed within California's *Lepechinia* a reticulate pattern of variously shared traits (e.g., leaf shape, calyx tube shape, calyx lobe shape), which he believed were derived from repeated episodes of range expansion, contact among populations, hybridization, range contraction, isolation of populations, and ultimately, drift and selection. Certainly, *L. rossii* fits this pattern.

Lepechinia rossii is geographically intermediate between populations of *L. calycina* (further west in the Topatopa, Mount Pinos, and Santa Ynez mountains of Ventura and Santa Barbara counties) and *L. fragrans* (to the southeast in the San Gabriel Mountains, or southwest in the Santa Monica Mountains). A comparison of relative ranges of these species is presented in Figure 1A. Although geographically intermediate between *L. calycina* and *L. fragrans*, the morphological features of *L. rossii* do not necessarily reflect a cline between those two taxa. The cauline leaves of *L. rossii* are most similar to *L. cardiophylla*, and to a lesser extent, *L. fragrans*, in shape, and to *L. cardiophylla* and *L. calycina* in general vestiture. The shape of the calyx in *L. rossii*, especially the relatively short, broad lobes, is more like that of *L. calycina*, versus the relatively long calyx lobes found in *L. fragrans*. The general inflorescence architecture, as well as size, shape, and orientation of the floral bracts are wholly unlike any of the Californian taxa, and appear unique within the genus (Averett 1993; Epling 1944; 1948; Munz 1959; 1974; Wiggins 1980).

Distribution

At present, only two *L. rossii* populations are known, one in the Liebre Mountains and one in the Topatopa Mountains, separated by a distance of ca. 40 km (Fig. 1A). Both populations are of relatively limited areal extent, which may explain their relatively late discovery. On the other hand, portions of both known populations are easily visible from long-established U.S. Forest Service roads. As suggested above, the earliest documented collections of *L. rossii* are likely those of B.W. Evermann or R. Hoffmann. Unfortunately, these three specimens lack definitive mature inflorescences and flowers, therefore providing limited information as to their identity. Previously, the Evermann and Hoffmann specimens had been tentatively identified as *L. calycina*. Apparently, due to their sterile condition, these specimens garnered little attention from subsequent workers, including Epling. Affinity with *L. rossii* is based on general provenance, leaf vestiture, and in the case of the Hoffmann specimen (SBBG #6303), incipient inflorescence morphology. Both Tar Creek and Pine Creek are tributaries of Sespe Creek, with their respective points of confluence with the main drainage separated by approximately 3.3 km. We believe the Evermann specimen was likely collected within a broader meta-population that includes the Tar Creek site. Although Hoffmann's locality information is so vague as to be anywhere within the Sespe drainage, we believe the specimen was taken within Sespe Canyon in the same general vicinity of Tar and Pine creeks.

Lepechinia rossii is the most narrowly distributed of the five Californian taxa, being endemic to the western Transverse Ranges (Fig. 1A). In contrast, *L. calycina* is the most widely distributed of the Californian taxa and is endemic to the state, ranging from southeastern Ventura County northward through the Coast Ranges to Lake County, eastward to Butte County, and southward through the foothills of the Sierra Nevada to Mariposa County (Averett 1993; Munz 1959, 1974; Smith 1998). *Lepechinia fragrans* is also endemic to the state, found on Santa Catalina (Los Angeles Co.), Santa Cruz, and Santa Rosa (Santa Barbara Co.) islands, and in disjunct occurrences on the mainland in the Santa Monica (Los Angeles and Ventura cos.) and San Gabriel (Los Angeles and San Bernardino cos.) mountains (Averett 1993; Junak et al. 1995; Munz 1959, 1974; Raven et al. 1986; Thorne 1967). *Lepechinia cardiophylla* is restricted to the Peninsular Ranges, found primarily in the northern Santa Ana Mountains (Orange and Riverside cos.), with small, widely disjunct populations to the south, in the coastal foothills of San Diego County and adjacent northwestern Baja California, Mexico (Averett 1993; Beauchamp 1986; Munz 1959, 1974; Lathrop and Thorne 1978; Wiggins 1980). *Lepechinia ganderi* is also restricted to the Peninsular Ranges, occurring in scattered populations in the higher coastal foothills of southwestern San Diego County and adjacent northwestern Baja California, Mexico (Averett 1993; Beauchamp 1986; Munz 1959, 1974; Wiggins 1980).

Habitat

Both the Red Mountain and Tar Creek populations of *L. rossii* occur within the Santa Clara River watershed, on lands managed by the U.S. Forest Service (Liebre Mountains, Angeles National Forest; Topatopa Mountains, Los Padres National Forest). In both areas, plants generally grow on north- to northeast-facing slopes, and on adjacent portions of ridgelines. There does not seem to be a strong geologic or edaphic factor involved in distribution of *L. rossii*. On Red Mountain, *L. rossii* is mainly associated with fine-grained, reddish, nonmarine sedimentary rock of Eocene or Paleocene age,

with outcrops of Precambrian gneiss and Mesozoic granitic rocks in the immediate vicinity (Jennings and Strand 1969). In the Tar Creek area, *L. rossii* is also associated with fine-grained, reddish substrate, but in this case marine sedimentary rocks of middle Miocene age, with outcrops of Oligocene volcanics in the general vicinity (Jennings and Strand 1969). Although the locality information on Evermann's 1917 collection of *L. rossii* is vague (Pine Creek near Sespe), geologic substrates in the area around Pine Creek and its confluence with Sespe Creek are dominated by middle Miocene volcanics, suggesting populations occur on this substrate as well. Hoffmann's 1927 collection has such vague locality information, that speculation on associated geologic substrate is unwarranted.

At both the Red Mountain and Tar Creek sites, *L. rossii* is associated with chaparral vegetation characterized by a mix of shrubs including *Adenostoma fasciculatum* Hook. & Arn., *Cercocarpus betuloides* Nutt. ex Torr. & A. Gray, *Clematis lasiantha* Nutt., *Eriodictyon crassifolium* Benth. var. *nigrescens* Brand, *Eriogonum fasciculatum* Benth. var. *foliolosum* (Nutt.) S. Stokes ex Abrams, *Eriophyllum confertiflorum* (DC.) A. Gray, *Fraxinus dipetala* Hook. & Arn., *Quercus berberidifolia* Liebm., *Heteromeles arbutifolia* (Lindl.) M. Roem., *Keckiella cordifolia* (Benth.) Straw, *Rhamnus ilicifolia* Kellogg, *Ribes malvaceum* Sm., and *Solanum xanti* A. Gray. As with other species of *Lepechinia* in California, *L. rossii* is generally associated with relatively open areas, often appearing in greatest abundance following wildland fire, or at least temporarily, in areas affected by anthropogenic disturbance, such as fuel breaks and road-cuts. Within mature stands of chaparral, *L. rossii* is largely limited to small natural openings, such as near bedrock outcrops, or within a gap where a larger shrub has died.

Conservation Status

Identifiable threats within the Liebre Mountains are largely limited to localized habitat disturbance by off-highway vehicle (OHV) activity, and maintenance of electric power line towers that cross the summit of Red Mountain. In the Topatopa Mountains, identifiable threats again include localized habitat disturbance by OHV activity, as well as grading of pads for petroleum exploration and potentially extraction. As a species associated with earlier phases of post-fire succession, of general concern is type-conversion of habitat due to invasion by weedy exotic grasses (e.g., *Bromus diandrus* Roth, *B. madritensis* L. subsp. *rubens* [L.] Husnot, *Vulpia myuros* [L.] C.C. Gmel.), and concomitant increase in fire frequency.

Acknowledgements

We express our sincere thanks to J. Travis Columbus (RSA), Dieter Wilken (SBBG), and Aaron Liston (OSC) for their encouragement to move forward with describing this *Lepechinia*; to SBBG and CAS for providing critical specimens on loan; to Valerie Soza, Lauren Raz, Amber Maurice, Tammy Morgan, and Valentin Arvizu for assistance in the field; and to Sula Vanderplank, Jennifer Cruse-Sanders, Naomi Fraga, and Gary Wallace for providing helpful comments on earlier drafts of the manuscript. Special thanks are extended to Naomi Fraga for her considerable assistance in producing the range map, to Elisha Mistretta for producing the line drawing, to Nancy Refulio for translation of the resumen, and to two reviewers for providing thoughtful comments and suggestions that have added significantly to the clarity and accuracy of this paper. Above all, we are forever indebted to Tim Ross for sharing with us, during countless hours of fieldwork conducted across southern California, his botanical knowledge, passion for plants, and keen wit.

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NOTEWORTHY COLLECTIONS

LATHYRUS HITCHCOCKIANUS Barneby & Reveal (FABACEAE).—Inyo Co., Death Valley National Park, Grapevine Mountains, head of Fall Canyon, 36°56′ 03″N, 117°07′10″W (NAD 27), 1980 m/6500 ft, 4 May 2001, *York 2576, with Davis* (DEVA). More than 100 plants observed on rhyolitic gravels with *Artemisia tridentata, Chrysothamnus parryi, Ephedra viridis, Juniperus osteosperma*, and *Pinus monophylla*.

Previous knowledge. This taxon was previously known from southern Nye County, Nevada. The Death Valley Expedition erroneously noted a collection from Wood Canyon in the Grapevine Mountains, 9 June 1891, *Funston & Coville 1760* (NY, UC) (F.V. Coville, 1893, Botany of the Death Valley Expedition, Contr. U.S. Nat. Herb. 4., Washington, DC) as being in Inyo County, California. Based on the expedition's map, the collection was actually made on the east side of the Grapevine Mountains in Phinney Canyon, Nye County, Nevada. There is no present-day Wood Canyon in the Grapevine Mountains. The upper elevations of the Grapevine Mountains are currently accessible by vehicle on historic mining roads from the Nevada side of the range. The canyons on the California side of the northern Grapevine Mountains are only accessible by foot and require scrambling around cliffs and dry falls. The only through roads are located in Titus and Boundary canyons in the southern Grapevine Mountains. The expedition did not travel through Titus Canyon, instead they left Death Valley traveling east up Boundary Canyon on 1 June 1891 (F.V. Coville, 1893, Botany of the Death Valley Expedition, Contr. U.S. Nat. Herb. 4., Washington, DC). Boundary Canyon is the divide between the Grapevine and Funeral mountains. It is the current location of the highway that links Death Valley with Beatty, Nevada.

Significance. This is the first documented collection from California.

ARABIS DAVIDSONII E. Greene var. *PARVA* Rollins (BRASSICACEAE).—Inyo Co., Death Valley National Park, Panamint Mountains, 600 m NE of Panamint Pass, 36°06′40″N, 117°03′53″W (NAD 27), 2540 m/8350 ft, 24 May 2001, *York 2639* (DEVA). A rare perennial with lavender corollas growing in the NW-facing crevices of a dry, exposed, granitic outcrop. With *Cercocarpus intricatus, Chamaebatiaria millefolium, Ephedra viridis, Holodiscus microphyllus, Ivesia saxosa*, and *Pinus monophylla*.

Previous knowledge. The holotype locality for *Arabis davidsonii* var. *parva* is 24 airmiles east-northeast of Kernville in Tulare County (R.C. Rollins, 1993, The Cruciferae of Continental North America, Stanford University Press, Stanford, CA). It was found in crevices of granite rocks on the crest of a ridge, 7500 ft, 9 June 1986, *Ertter 6363, with Holland and Dains* (GH, UC). Its also been reported to the south in Kern County and to the north in the Sierra Nevada in rocky outcrops along the trail from Willow Lake to South Fork Big Pine Creek canyon, at an elevation of 2770 m/9100 ft on 6 July 1977 (*Taylor 6586*, JEPS 90207).

Significance. Although Rollins did not include this variety in the most recent treatment of California's flora (J.C. Hickman, 1993, The Jepson manual: Higher plants of California, University of California Press, Berkeley, CA), his description in his North American treatment of Brassicaceae (R.C. Rollins, 1993, The Cruciferae of Continental North America, Stanford University Press, Stanford, CA) exactly describes the diminutive plants found in the Panamint Mountains. The plants retain this character at all three separate populations observed by the author in Death Valley National Park. This extends the known range into the desert mountains 88 km east from the type locality, and 122 km east from the other Inyo County population.

PERITYLE VILLOSA (S.F. Blake) Shinn. (ASTERACEAE).—Inyo Co., Death Valley National Park, Panamint Mountains, Johnson Canyon, 1.7 km NW of Hungry Bills Ranch, 36°06′02″N, 117°03′11″W (NAD 27), 1860 m/6110 ft, 23 May 2001, *York 2628* (DEVA). A locally common perennial not yet flowering growing on a partially-shaded, N-facing, calcareous outcrop. With *Artemisia tridentata, Eriogonum heermannii, Juniperus osteosperma, Peraphyllum ramosissimum, Pinus monophylla*, and *Prunus fasciculata*.

Previous knowledge. Endemic to the mountains of Death Valley National Park. Found in crevices in carbonate rock outcrops in the Panamint, Cottonwood, and Grapevine mountains. First collected in the middle fork of Hanaupah Canyon, Panamint Mountains, at an elevation of 2090 m/6860 ft on 22 September 1931 (*Coville & Gilman 108*, U.S. 1531290).

Significance. First collection made in the Panamint Mountains since 1935. Extends the known range approximately 11 km south.

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CALIFORNIA

CRYPTANTHA LEIOCARPA (Fischer & C. Meyer) E. GREENE (BORAGINACEAE).—Orange Co., along the coast at Newport Beach on back dunes southeast of Balboa Pier. Thousands of plants in the area from the parking lot at the pier southeast and down the coast nearly to the west jetty at the entrance to Newport Bay. Found with *Ambrosia chamissonis, Cakile maritima, Camissonia cheiranthifolia, Calystegia soldanella, Abronia umbellata*, and *Distichlis spicata*. Population centered at foot of "E" Street (UTM 11S 0416939E 3718062N NAD83; deposited at RSA, duplicates to be distributed).

Previous knowledge. *Cryptantha leiocarpa* is known from southern Oregon (Gold Beach) south to northern Santa Barbara County at Surf, north of Point Conception (I.M. Johnston, 1925, Studies in the Boraginaceae, Contributions from the Gray Herbarium of Harvard University). According to Smith (1998, A Flora of the Santa Barbara Region, California, 2nd ed.), found "about dunes at Point Conception, Point Arguello, Surf, Casmalia, and Oso Flaco Lake." On the

Channel Islands, the species has been collected from Santa Rosa Island (G.D. Wallace, 1985, Contributions in Science, No. 365, Natural History Museum of Los Angeles County). It was also reported from San Miguel (Greene 1887, Pittonia 1:74–93) and Santa Cruz Islands (Greene 1887, Bull. Cal. Acad. Sci. 2:377–417), though voucher specimens have not been located, and the species has not been found on Santa Cruz Island recently (Junak et al. 1995, A Flora of Santa Cruz Island). Reported as far south as the northern "South Coast" of California by Kelley and Wilken (1993, in The Jepson Manual), and to Playa del Rey, Los Angeles County, by Jepson (1912), though these and other southerly reports were likely confused with *Cryptantha hispidissima* (I. M. Johnston 1925). C. *hispidissima* was reduced to varietal status by Johnston (Munz 1935, Man. So. Cal. Bot.), but has been treated as a synonym of *C. clevelandii* var. *florosa* (e.g., Abrams 1951, Illus. Flora Pac. States, Vol. III). This variety, recognized in the floristic treatments of Munz (1959 and 1974), is not recognized as distinct from *C. clevelandii* by Kelly and Wilken (1993). Previously collected from coastal sandy soils and dunes.

Significance. This is the first verified mainland record south of Point Conception. A large population occurs at this site in a relatively extensive dune system. This site also sustains one of the few extant coastal dunes remaining in Los Angeles or Orange counties, with several other locally uncommon taxa.

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WASHINGTON

MELICA CILIATA L. (POACEAE).—King Co., dry sand, waste ground, industrial area near cement factory, Duwamish River mouth, Riverside, Seattle, 47°34.2′N, 122°20.7′W, elev. 3 m, 13 Aug 2003, *Wechsler s.n.* WTU; dry basalt fill, riverbank, same site, 16 June 2004, *Zika 19860* (NY, UC, WTU).

Previous knowledge. Silky melic is native to Eurasia, where it often favors calcareous substrates. It is occasionally planted as an ornamental in North America. Its spread from cultivation in Riverside may have been facilitated by cement processing waste.

Significance. First record as an escape from cultivation in Washington. Apparently the first report of this species reproducing outside of gardens in North America (Hitchcock, A. S. & A. Chase. 1971. Manual of the Grasses of the U.S., 2nd ed. Dover Publications, New York. Kartesz, J. T. and C.A. Meacham. 2004. Synthesis of the North American Flora, CD-ROM Version 2.0. Published by J. T. Kartesz & Phylosystems Corporation, Chapel Hill. Soreng, R. J., P. M. Peterson, G. Davidse, E. J. Judziewicz, F. O. Zuloaga, T. S. Filgueiras, and O. Morrone. 2003. Catalog of New World Grasses (Poaceae): IV. Subfamily Pooideae. Contributions from the U.S. National Herbarium 48: 1–730. Web Grass Manual, accessed January 2006, http://herbarium.usu.edu/webmanual/). Its potential invasiveness should be examined.

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CONTRIBUTIONS TOWARD A BRYOFLORA OF CALIFORNIA III. KEYS AND ANNOTATED SPECIES CATALOGUE FOR LIVERWORTS AND HORNWORTS

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ABSTRACT

Keys are provided to 54 genera, 142 species, 6 infraspecific taxa, and 3 undescribed species of California liverworts and hornworts within 33 families. In addition, 3 genera and 16 species previously reported have been excluded from the California bryoflora. The keys emphasize gametophytic characters. Annotated comments for each species focus on what to look for and how to separate it from species with similar morphology. The worldwide and California distribution of each species is provided.

Key Words: California, flora, liverworts, hornworts, keys, species, distribution.

I like to look on plants as sentient beings, which live and enjoy their lives—which beautify the earth during life and after death may adorn my herbarium. When they are beaten to a pulp or powder in the apothecary's mortar, they lose most of their interest for me. It is true that the Hepaticae have hardly as yet yielded any substance to man capable of stupefying him or of forcing his stomach to empty its contents, nor are they good for food; but if man cannot torture them to his uses or abuses, they are infinitely useful where God has placed them, as I hope to live to show, and they are, at the least, useful to, and beautiful in themselves—surely the primary motive for every individual existence.

R. Spruce, *Notes of a Botanist on the Amazon and Andes* (ed. A.R. Wallace). London. 1908. Vol 1: xxxix.

Over 100 years has passed since the publication of *The Hepaticae and Anthocerotes of California* by M. A. Howe (1899) who recognized 36 genera and 86 species. Many additional species have since been added to our flora, taxonomic revisions have resulted in name changes, and distributional patterns are better understood. Now, 54 genera and 142 species are recognized and three new species await formal description. The liverwort and hornwort flora of California can be displayed and analyzed from different perspectives. There are 12 genera included in the complex thalloid liverwort group, three genera in the sphaerocarpoid group, seven genera in the simple thalloid group, 29 genera in the leafy liverwort group, and three genera in the hornworts (Table 1). Of the 54 genera in this catalogue, 26 genera are represented in the state by a single species. The largest liverwort genera in California include *Riccia* (13 species), *Lophozia* (11), *Scapania* (10), *Jungermannia* (9), *Cephaloziella* (6), and *Calypogeia*, *Frullania* and *Marsupella* (each with 5). These eight genera contain just under 50 percent of the liverwort flora of California.

This publication is a companion to the two publications on California mosses by Norris and Shevock (2004a, b). These three publications provide reference points for future research on the California bryoflora. Several regions of the state (e.g., Mojave and Sonoran Deserts, Sacramento and San Joaquin Valleys, and east side of the Sierra Nevada) and most counties still are in need of careful, intensive study. New additions (including new species) to the state's bryoflora are sure to be found with continued exploration and collection.

Although weedy or introduced liverworts and hornworts are uncommon in California, the potential of exotics becoming established is great in urbanized areas, especially in the coastal counties where a great diversity of introduced ornamental plants are grown coupled with a more moderate climate during the summer months. The threat is somewhat reduced by the summer drought typical of our Mediterranean climate. However, landscaped parks, convention grounds, and botanical gardens that use summer watering regimes can be sources for non-native bryophyte introductions.

The purpose of this publication is to help beginning students, public agency botanists, environmental consultants, and amateur and professional bryologists to accurately name liverworts

TABLE 1. SYNOPSIS OF FAMILIES AND GENERA OF LIVERWORTS AND HORNWORTS OCCURRING IN CALIFORNIA.

Liverworts		Hornworts
Aneuraceae	**Lepidoziaceae**	**Anthocerotaceae**
Aneura	*Bazzania*	*Anthoceros*
Riccardia	*Kurzia*	**Notothyladaceae**
Antheliaceae	*Lepidozia*	*Phaeoceros*
Anthelia	**Lunulariaceae**	*Phymatoceros*
Aytoniaceae	*Lunularia*	
Asterella	**Marchantiaceae**	
Cryptomitrium	*Marchantia*	
Mannia	*Preissia*	
Reboulia	**Metzgeriaceae**	
Blasiaceae	*Metzgeria*	
Blasia	**Pallaviciniaceae**	
Calypogeiaceae	*Pallavicinia*	
Calypogeia	**Pelliaceae**	
Cephaloziaceae	*Pellia*	
Cephalozia	**Plagiochilaceae**	
Cephaloziellaceae	*Plagiochila*	
Cephaloziella	**Porellaceae**	
Cleveaceae	*Porella*	
Athalamia	**Pseudolepicoleaceae**	
Conocephalaceae	*Blepharostoma*	
Conocephalum	**Ptilidiaceae**	
Fossombroniaceae	*Ptilidium*	
Fossombronia	**Radulaceae**	
Frullaniaceae	*Radula*	
Frullania	**Ricciaceae**	
Geocalycaceae	*Riccia*	
Chiloscyphus	*Ricciocarpos*	
Geocalyx	**Riellaceae**	
Lophocolea	*Riella*	
Gymnomitriaceae	**Scapaniaceae**	
Gymnomitrion	*Anastrophyllum*	
Marsupella	*Barbilophozia*	
Gyrothyraceae	*Diplophyllum*	
Gyrothyra	*Douinia*	
Jungermanniaceae	*Lophozia*	
Gymnocolea	*Scapania*	
Jungermannia	**Sphaerocarpaceae**	
Mylia	*Geothallus*	
Nardia	*Sphaerocarpos*	
	Targioniaceae	
	Targionia	

and hornworts, to document what and where they have been found, and to aid in the recognition of them as significant components of California's amazingly diverse flora. Not only is the search for and identification of liverworts and hornworts fulfilling in its own right, it also is an area in which beginners and amateurs can make significant contributions to the field of bryology and floristics (Kellman 2003). Liverworts and hornworts are small plants. Their study requires an innate appreciation of things small and a willingness to spend time to seek them out in their microhabitats in the field. With practice and experience, many genera and species can be recognized in the field with a high level of certainty. However, because of their small size, most liverworts and hornworts will need to be examined under a microscope to observe diagnostic features used for species recognition. Therefore, collecting samples for identification confirmation is necessary.

HOW TO DISTINGUISH LIVERWORTS AND HORNWORTS FROM MOSSES

Bryophytes (bryo- = moss; phyt- = plant). Historically, the term bryophytes collectively refers to mosses, liverworts and hornworts, which are land plants that lack lignified water-conducting tissue and reproduce by spores, rather than by seeds. They have similar life history strategies consisting of two distinct multicellular generations: 1) a free-living, longer-lived gamete-producing generation (called a gametophyte) and 2) a shorter-lived, spore-producing generation (called a sporophyte), which, during its development, remains attached to the gametophyte and produces a single capsule (sporangium).

In the field, mosses can be confused with leafy liverworts. With experience, however, the two groups usually are easily separated based on texture and growth characteristics that are easier to see than to describe.

The following features separate liverworts and hornworts from mosses:

Liverworts and Hornworts

- adult gametophytes leafy or thalloid, when leafy usually bilaterally symmetrical;
- leaves, when present, without a midrib (= costa);
- oil-bodies usually present in liverworts and absent in hornworts;
- leaves of many species lobed;
- rhizoids unicellular;
- sporophytes either lack a meristem (liverworts) or have one between the foot and capsule (hornworts).

Mosses

- adult gametophytes leafy and mostly radially symmetrical;
- leaves of most species with a distinct midrib (= costa);
- oil-bodies always absent;
- leaves not lobed;
- rhizoids uniseriate filaments;
- sporophytes with an apical meristem.

Serious students seeking to acquire a bryological library should obtain 1) the introductory bryophyte biology textbook by Schofield (1985), which provides detailed information about the major bryophyte groups, including helpful aids in the study of these plants, 2) the excellent reference book by Crum (2001), which is for more advanced students, and the six volume treatise by Schuster (1966–1992), which contains detailed descriptions of liverworts and hornworts of North America east of the hundredth meridian.

Specimen Collection, Preservation and Examination

What equipment is needed to bring voucher specimens back for identification? Basic needs include 1) a 10× to 20× hand lens, 2) a small knife or wood chisel, and a small spatula or putty knife to carefully extricate bryophytes from the substrate, 3) small flexible containers to hold individual specimens, and 4) pencil and paper to record field data. Recommended is an inexpensive, hand-held GPS to obtain elevation, latitude and longitude.

Your collection documents a species in a specific habitat and location at a point in time. Survey the population **before** making a collection. Is it a small, localized population or widely distributed in that habitat? A good rule of thumb: never take more than five percent of a colony or population. Make your collection an important research tool: 1) Except for rare species or small populations, collect more than a pinch. Collect enough plant material to show possible morphological variation; 2) Search populations for antheridia, archegonia, sporophytes, and gemmae because they can be significant aids in species identification; and 3) When a population occurs in a varying habitat (e.g., marshy areas with wet depressions and drier sides and tops of hummocks) include plants representing these different microhabitats. The color and form of plants of the same species can markedly vary when growing in wet, shaded, or drier microenvironments. Make good field notes and keep them with the specimens. The lasting value of the specimen is greatly enhanced with a detailed label that includes information on who collected it, when and where was it collected, what was it growing on, how common was it, and specific locational directions to the site.

It is essential that each collection be kept separate and separately labeled (except in inclement weather, when mixed collections should be sorted and labeled immediately upon return to a dry environment). Many bryologists use a numbered and folded paper specimen packet, or a paper #2 cargo or sandwich bag. Field collection data (including locality, habitat, substrate, and date) can be written in pencil directly on the bag or on a slip of paper and placed with the specimen. Some bryologists bring them back alive in plastic bags. Favored are the old-fashioned small plastic Baggies, which lack the zip-lock. Field data are placed in the Baggie with each voucher. At the end of the day, the live specimens can be placed in an ice chest (for a few days with no adverse effect) until return home.

Whichever collecting technique is used, it is really important to develop the habit of looking at the specimens under the microscope while they are still fresh. Doing so will expedite eventual identification. For microscope observations, clean plants of attached substrate so that rhizoids, scales and/or underleaves can be observed. In addition, oil-bodies in several genera (e.g., *Calypogeia, Lophozia, Nardia, Riccardia,* and *Scapania*) disappear in dry specimens and oil-body information is important for the identification of these genera. Even when oil-bodies are still visible in dry specimens, their form, number, and color can change in the drying process. For oil-bodies, record presence or absence, their distribution in a leaf or thallus, range and average number per (usually mid-leaf) cell, form, and their approximate size and color. Keep this information in the packets with the collections and develop the labels.

Note. Living plants kept too long, and plants dried too slowly can become etiolated or moldy. Specimens should be air-dried as soon as possible (do not use artificial heat), and plants never should be pressed flat. Once the specimens are dried and identified, then they can be transferred into archival quality packets. Use 100 percent cotton, acid-free paper for your permanent herbarium specimen packets. Duplicates of your collections can be made available to other researchers or for placement in a herbarim. Because most herbaria have their own curatorial procedures, these duplicates can be provided in standard photocopy paper, but enclose a label printed on at least 25 percent cotton fiber paper.

As with mosses, identification of liverworts and hornworts usually requires access to both a compound and a dissection microscope. The compound microscope should be fitted with an ocular micrometer in order to measure leaf, cell and spore sizes. Paton (1999) contains detailed data on measurements, including illustrations. Leaf Measurements. Occasionally, the length and width of a leaf must be compared (e.g., some species of *Jungermannia*). For leaf length, measure from the approximate middle of its insertion line on the stem to a) the apex of a pointed leaf, b) the midpoint of the leaf margin with a broadly rounded apex, or c) the midpoint of an imaginary line between the apices of a bilobed leaf or two longest lobes of a multilobed leaf. For leaf width, measure the widest part of the leaf at right angles to the leaf length. Cell Measurements. Cell length is measured along the axis generally parallel to the length of the leaf, leaf lobe or midrib (of thalloid plants). Cell width is measured at right angles to cell length. Exception. The direction of measurement of leaf and thallus marginal cells is an exception to cell length and width measurements described above. The width of marginal leaf and thallus cells is measured parallel to the margin of the leaf or thallus. In this publication, measurement of cell length and width includes the lumen and ½ the wall thickness on each side of the lumen. Spore Measurements. Spore diameter is measured on spores viewed from the distal or proximal face (See Appendix 1 for definition of terms). Measurement of spore diameter includes ornamentation of the spore coat. Measure fully mature, ready to discharge spores, because in some plants (e.g., *Fossombronia*), deposition of wall ornamentation material occasionally continues late during sporophyte maturation and seta elongation.

Occasionally, a thallus or stem requires cross-sectioning in order to examine details of internal structure. The senior author uses the following technique: 1) place a fresh or hydrated thallus or stem on a glass slide; 2) place your thumb gently but firmly on the specimen, parallel to the long axis of the specimen; 3) with a single-edge razor blade under a low power of the dissection microscope, use your thumb tip to guide the blade when cutting a section, the first section then is discarded; 4) with a slight chopping motion, begin to cut thin sections by slowly pushing the razor blade back against your thumb tip as sections are cut; 5) discard the remaining plant material and any sections that appear to be too thick; and 6) add a small drop of water and cover slip, and observe under the compound microscope. With experience and practice thin sections of thalli and stems are quickly produced.

Geographic Regions of California

The geologic history of California is complex and its geography varied—from the coast to the high Sierra Nevada, and from the temperate rain forests of the northwest to the southeastern deserts. This tremendous diversity in substrates, habitats, microenvironments and "higher" plant communities all serve to influence the distribution of liverworts and hornworts. (For detailed information about California's geology, plant life and natural history, see Oakeshott 1978; Ornduff et. al. 2003; and Schoenherr 1992). Figure 1 locates the 11 Geographic Regions used in this publication (modified from the 10 used by Norris and Shevock [2004a]; the Northwestern California Region used by them has been separated into the Klamath Ranges and the North Coast Region).

1. Klamath Ranges (KR). The KR rock types are similar to those of the Sierra Nevada, i.e., remnants of metamorphic and volcanic rocks intruded by granite (Oakeshott 1978), and include the Marble, Scott and Siskiyou Mountains, and Trinity Alps. The Klamath Ranges extend from Oregon south to the South Fork Mountain Fault Zone, essentially the line followed by the Klamath and

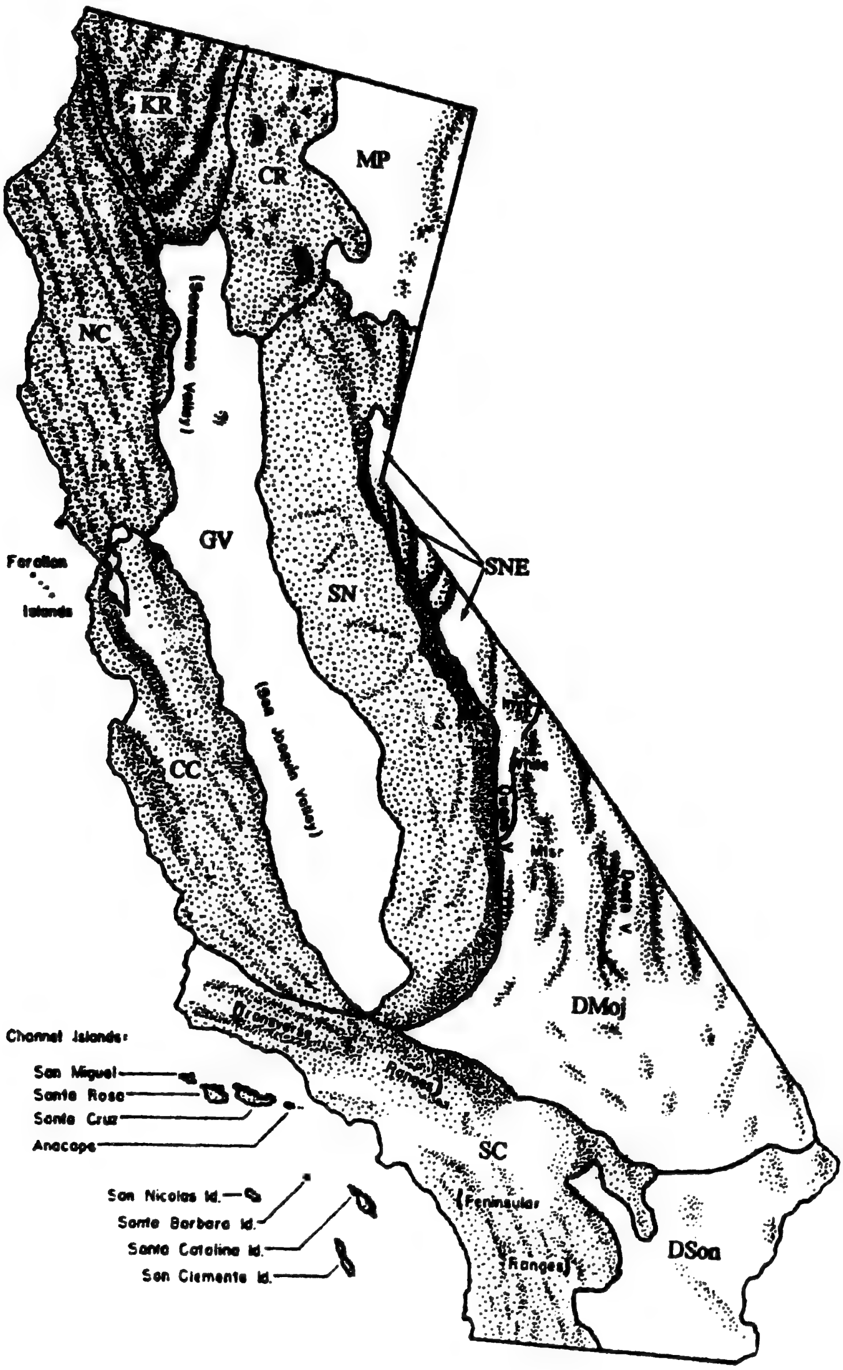

FIG. 1. California Geographic Regions. **CC**—Central Coast Region; **CR**—Cascade Range; **DMoj**—Mojave Desert; **DSon**—Sonoran Desert; **GV**—Great Valley; **KR**—Klamath Ranges; **MP**—Modoc Plateau; **NC**—North Coast Region; **SC**—South Coast Region; **SN**—Sierra Nevada; and **SNE**—Sierra Nevada East. (Modified from Munz, P. A. 1973. *A California Flora and Supplement*. UC Press, Berkeley, CA).

Trinity Rivers east to Douglas City, and then follow State Highway 299 from Douglas City east to Redding. The KR includes the area between the Del Norte County coast east to Interstate Highway 5 at Redding to the Oregon border.

2. North Coast Region (NC). The NC Region extends from South Fork Mountain Fault Zone-Redding south to the San Francisco Bay, and from the coast east to the Great Valley. Included are

Yolla Bolly, Snow Mountain, King Range, Mendocino Range, Mayacmas Mountains, Mount Tamalpais, and the Marin Peninsula.

3. Central Coast Region (CC). The CC Region extends from the San Francisco Bay south to State Highway 166 (on the north side of the Santa Ynez Mountains), and from the coast east to the Great Valley. Included are Diablo, Gabilan, Santa Lucia, and La Panza Ranges, and the Santa Cruz Mountains.

4. South Coast Region (SC). The SC Region extends from State Highway 166 south to Mexico, and from the coast east to the Mojave and Sonoran Deserts, and encompasses the Transverse and Peninsular Ranges. Included are the Santa Ynez, San Gabriel, Santa Monica, San Bernardino, San Jacinto, Santa Margarita, Santa Rosa, Laguna, Santa Ana, Agua Tibia, Cuyamaca, and In-Ko-Pah Mountains.

5. Cascade Range (CR). The CR region represents the southern end of a long north-south volcanic chain that extends from Southern British Columbia through Washington and Oregon into northern California. Included are Mount Shasta and Mount Lassen. Interstate Highway 5 north of Redding and the Great Valley form the western boundary. The southern boundary is complex, following an east to west line starting about where State Highway 44 joins State Highway 36 east of Susanville; it then follows State Highway 36 until it joins State Highway 32, and then follows Highway 32 until it reaches the Great Valley.

6. Sierra Nevada (SN). The SN Region represents a great block of granitic rock, with remnants of metamorphic and volcanic rocks. The Great Valley is its western border; the East of Sierra Nevada Region and the northwestern part of the Mojave Desert form the eastern border; the Klamath Range and Modoc Plateau form its northern border; and the Mojave Desert forms its southern border. The Sierra Nevada Region extends south to, and includes, the Tehachapi Mountains.

7. Great Valley (GV). The GV Region includes the Sacramento and San Joaquin Valleys.

8. Modoc Plateau (MP). The MP is an undulating volcanic landscape and is considered to be a small southwestern corner of the Columbia Plateau of eastern Oregon, Washington and southern Idaho. The boundaries of Modoc Plateau are Oregon on the north, Cascade Range on the west, Sierra Nevada on the south, and the State of Nevada on the east. The Warner Mountains are an uplifted section on the east side of the Modoc Plateau.

9. East of Sierra Nevada (SNE). The SNE Region includes the parts of Alpine and Mono Counties east of Sierra Nevada, and a part of Inyo County between Sierra Nevada and the Mojave Desert. The Sweetwater Mountains, Bodie Hills and Mono Lake are included in the East of Sierra Nevada Region.

10. Mojave Desert (DMoj). The DMoj Region includes the Inyo, White, Panamint, Funeral, New York, Clark, Last Chance, and Providence Mountains, Joshua Tree National Monument, and the Kingston Range. The Mojave Desert extends east into Nevada and Arizona.

11. Sonoran Desert (DSon). The DSon Region extends from the South Coast Region east into Arizona. The Pinto Basin is considered to be the western border of DSon. It includes Anza-Borrego Desert State Park, Palm Springs and the Chocolate Mountains. The California portion of the Sonoran Desert often is called the Colorado Desert.

Taxonomic Considerations

In early taxonomic treatments, hornworts were grouped with liverworts in the Hepaticae. Now it is recognized that liverworts and hornworts are not closely related and they are placed in separate phyla: Marchantiophyta (liverworts) and Anthocerotophyta (hornworts) (see Shaw and Goffinet [2000] for details). The informal names of liverworts and hornworts will be used here.

The genus and species names used, the citations of authors of species names, and the grouping of genera into families, are based on Stotler and Crandall-Stotler (1977), Grolle (1983), Crandall-Stotler and Stotler (2000), and Stotler and Crandall-Stotler (2005a), and updated as new information became available. Table 1 depicts the taxonomic grouping of genera within the families of California liverworts and hornworts.

Keys and Species Catalogue Overview

Key design. The following keys are hierarchical, organizing the bryoflora into smaller and smaller units. The first key separates liverworts from hornworts. Each group is treated separately in sections that follow. Liverworts are a large and diverse group. Because classification of the upper ranks of

liverworts presently remains unresolved, the first key under LIVERWORTS separates this large group into four informal sub-groups: 1) Complex Thalloid Liverworts, 2) Sphaerocarpoids, 3) Simple Thalloid Liverworts and 4) Leafy Liverworts. These categories are used for the convenience of ordering information for key purposes only and do not imply close phylogenetic relationships of all genera within a sub-group. When the sub-group to which your specimen belongs is known (e.g., Complex Thalloid Liverworts), then turn directly to the Genus Key of that sub-group in order to identify the genus. If you know the sub-group and genus, but not the species, turn to the Species Key under that genus. The genera are alphabetically listed under each sub-group.

Hornworts are a small group. Under HORNWORTS the keys by-pass sub-groups and go directly to genus and species (this section follows the liverworts).

Gametophytes of many species of liverworts and hornworts exhibit great morphological variability in response to local environmental conditions. In branching pattern and color, for example, a hornwort growing in a wet, reduced light habitat can look quite different from the same species growing in a drier, exposed habitat. Diseased individuals or plants collected early in its growing season (e.g., from November – February, following the variable onset of the California rains) can look different from healthy, mature (typical) shoots. Because a key character is not always present in all plants in a population, the cautionary words "sometimes," "usually," "mostly," "often," and "rarely" are used as reminders that variation does occur. It is important to select healthy, robust, mature parts of the plant for study, and to carefully read the keys.

Books with species illustrations are invaluable aids in identification. A must is Schofield (2002), *Field Guide to Liverwort Genera of Pacific North America.* (In this book, hornworts are included in the term liverwort). This useful book includes a full-page illustration of one species as a representation for each genus. Many species of California liverworts and hornworts are illustrated in this publication. Also recommended are the books by Paton (1999) and Damsholt (2002); although about British Isles and Nordic liverworts and hornworts they contain high quality and very detailed illustrations of many species that also occur in California. The six volume work by Schuster (1966–1992) on the liverworts and hornworts of North America east of the hundredth meridian also is an invaluable, but expensive resource; in addition, most of these volumes are out-of-print.

An effort throughout this work presented here has been made to keep scientific terminology to a minimum in order to focus on species identification, not on vocabulary. However, scientific terminology is more precise and provides a more accurate description. Appendix 1 contains a GLOSSARY of terms used in this publication.

Annotated species catalogue. A key is only a guide, a short-cut to plant identification. Annotation comments permit discussion about variation and potential problems in identification of each species. This publication is not designed as a manual, in which the same type of information is listed for each species. Instead, comments are crafted for individual species. The following categories enable us to share our experience in working with California liverworts and hornworts: **1) Distinctive features**—or what are the most important characteristics to look for in vegetative and reproductive plants. This section provides more detailed information about variation within a species than occurs in the key; **2) Separation**—how to descriminate a specimen from others that can look similar. For example, some dry plants of *Targionia hypophylla* can resemble some dry plants of *Asterella bolanderi*; a simple thallus cross-section can be used to separate these two plants; **3) Illustrations**—this publication does not provide illustrations. This section prresents references where high quality illustrations are available for visual comparison with your specimen; **4) Habitat**—often it is reassuring to know that your specimen was collected in the usual habitat. This section summarizes the types of habitats and at what elevations this species has been found previously; and 5) **Distribution**—this section summarizes the published worldwide distribution of the species, with particular reference to those California Geographic Regions in which it has been collected previously. A herbarium specimen is cited to document the regional distribution of each species.

Even with additional species information, be prepared for occasions when identification remains in doubt. Liverworts and hornworts are noted for the morphological variability of their gametophytes. Temporary changes in environmental conditions can produce dramatic changes in thallus and shoot color, leaf position, shape and size, leaf decurrency on the stem, development of cilia or trichomes, and cell wall thickness. In addition, juvenile growth forms of some species (of collections made too early in its growing season) often do not fit the key. Specimens that do not key to a known species can be a) a morphological variant of a known species, b) a species new to California, or c) an undescribed (new to science) species. Such collections often can be sent to a professional bryologist, along with full collection data and sufficient material for the bryologist to retain a portion of the collection to be placed in a herbarium so that the record is documented and is available to other researchers. **Important:** Write first. Communicate with any expert or professional before sending material.

There are times when research in progress requires use of caution in the circumscription of a species. In *Conocephalum conicum*, published preliminary research indicates that this taxon is comprised of more than one species (Szweykowski et al. 2005). Most of these new species cannot be morphologically separated. In *Marchantia polymorpha* research combining morphological studies and experimental techniques support the existence of three subspecies, but specimens can be assigned with certainty only when experimental data are available (Bischler-Causse and Boisselier-Dubayle 1991). In cases such as these examples, we use the species name in a broad sense (=*sensu lato* = *s. l.*), in contrast to a narrow sense (=*sensu stricto* = *s. str.*).

Liverwort and hornwort specimens at ABSH, CAS, CHSC, and UC, and in the personal herbarium of the senior author were the primary source for this study. We also examined specimens at COLO, DAV, MO, NY, SFSU, SFV, WTU, and YU. The Doyle herbarium is being transferred to UC.

Appendix I contains a glossary of terms as used in this publication. Appendix II is a list of synonyms of liverworts and hornworts reported for California.

Liverwort or Hornwort

1. Plants leafy or thalloid; cells of the apical region with many small chloroplasts per cell; capsules spherical to elongate, lacking stomata and a central columella. . . . . **Liverwort** p. 8.
1. Plants always thalloid; cells of the apical region with a single chloroplast per cell (some species have two or more chloroplasts in cells of other parts of the thallus); capsules elongate, long cylindrical (horn-like), with stomata and a central columella. . . . . . . **Hornwort** p. 97.

LIVERWORTS

Key to the Four Major Groups of Liverworts

1. Plants thalloid, with internal air chambers or vertical, finger-like air-channels; rhizoids of most species both pegged and smooth-walled. . . . . **Complex Thalloid Liverworts** p. 8.
1. Plants leafy or, if thalloid, without internal air chambers or vertical, finger-like air-channels; rhizoids always smooth-walled. . . . . **2.**
2. Plants leafy, only rarely dichotomously branched; archegonia and sporophytes terminal on the main axis or lateral branch. . . . . **Leafy Liverworts** p. 45.
2. Plants thalloid or, if leafy, dichotomously branched; archegonia and sporophytes on the dorsal surface of a main axis or lateral branch. . . . . **3.**
3. Plants **either** terrestrial with bottle- or flask-shaped involucres covering the dorsal surface, **or** ribbon-like submerged aquatics attached to the substrate. . . . . **Sphaerocarpoids** p. 31.
3. Plants terrestrial but never with bottle- or flask-shaped involucres on the dorsal surface. . . . . **Simple Thalloid Liverworts** p. 36.

Complex Thalloid Liverworts

Gametophytes of California species of complex thalloid liverworts are distinguished by a) a dorsiventral thallus with differentiated internal photosynthetic tissue consisting of air-chambers or vertical, finger-like air-channels, b) usually two kinds of rhizoids—pegged, with localized internal deposits of wall material and smooth-walled, lacking such deposits, and c) unistratose scales usually on the ventral thallus surface (these scales are obsolete or ephemeral in a few species).

The dorsiventral gametophytes of hornworts and simple thalloid liverworts a) lack differentiated internal photosynthetic tissue with air-spaces, b) have only smooth-walled rhizoids and c) usually lack unistratose scales.

In California, there are 12 genera, 28 described species, 1 species to be described in a subsequent publication, and 2 previously reported species excluded from the flora.

Genus Key (See Appendix I, Glossary, for definition of terms)

The first key is to be used for plants with sporophytes. Plants are more easily identified to genus when the key includes a combination of vegetative and sexual reproductive features. For this reason, try to plan field-work around the seasonal reproductive biology of the plants and search thoroughly for this year's or the previous year's reproductive structures before making a collection. In general, collections are best made from mid-March to late May in lower elevation, summer-dry habitats, and June to September in higher elevation, slow-to-dry or snow-melt areas.

The second key is to be used for plants that lack sporophytes. Because of vegetative thallus morphological and structural diversity within a genus, some species of the same genus will key at different places (e.g., species of *Riccia*). Moreover, the genera of *Mannia*, *Reboulia* and *Asterella* belong to the same family and, at times, can be very difficult to separate without the availability of reproductive structures; for these three genera the key goes directly to species.

I. Plants With Sporophytes

1. Archegonia and sporophyte capsules embedded in thallus tissue; sporophytes consisting of a capsule only (without a seta or foot); capsules containing spores but not sterile cells (elaters). . . . . **2.**
1. Archegonia and sporophyte capsules associated with an archegoniophore or involucre, but never embedded in thallus tissue; sporophytes consisting of a capsule, seta and foot; the capsules containing spores and sterile cells (elaters). . . . . **3.**
2. Plants floating like a canoe or raft on the water surface, ventral scales conspicuous, purplish, pendant and lanceolate, or plants stranded with ventral scales smaller, inconspicuous, and purplish to hyaline; oil-cells scattered in the dorsal epidermis and ventral scales; thalli of male plants with elongate antheridial receptacles in the dorsal grooves. . . . . **Ricciocarpos**
2. Plants terrestrial, or if aquatic, floating at or just below the water surface; ventral scales minute, vistigial or larger and projecting beyond the thallus margins; oil-cells absent in the dorsal epidermis and ventral scales; antheridia scattered in the dorsal thallus tissue, but never in a differentiated receptacle. . . . . **Riccia**
3. Sporophytes sessile, displaced to the ventral surface at a branch apex and enveloped by a conspicuous, shiny, purplish-black involucre. . . . . **Targionia**
3. Sporophytes elevated on an archegoniophore above the thallus surface, not enveloped by a conspicuous, shiny, purplish-black involucre. . . . . **4.**
4. Thallus dorsal epidermis with compound pores; antheridia elevated on antheridiophores above the thallus. . . . . **5.**
4. Thallus dorsal epidermis with simple pores; antheridia in receptacles or scattered on the dorsal thallus surface, not elevated on antheridiophores. . . . . **6.**
5. Carpocephalum with 7–11 finger-like rays (resembling spokes of an umbrella); thalli often with dorsal cup-shaped gemma-receptacles; ventral scales in 4–6 rows (2–3 rows on each side of the midrib), with oil-cells. . . . . **Marchantia**
5. Carpocephalum without finger-like rays; thalli without gemma-receptacles; ventral scales in 2 rows (1 row on each side of the midrib), without oil-cells. . . . . **Preissia**
6. Thallus air-chambers in a single layer, with uniseriate chlorophyllose filaments attached to the chamber floor; ventral scales each with a single, semicircular appendage. . . . . **7.**
6. Thallus air-chambers in more than one layer, empty of filaments, but often subdivided by cell-plates or secondary walls (the photosynthetic tissue often appearing spongy); ventral scales each with 1–4 slender appendages. . . . . **8.**
7. Thalli large, to 25 cm long and 17 mm wide; fresh thalli generally fragrant when crushed; terminal cells of photosynthetic filaments under pores markedly elongate and somewhat pyriform in shape; carpocephalum conical at maturity; gemma-receptacles absent. . . . . **Conocephalum**
7. Thalli smaller, 1.5–4 cm long and 5–10 mm wide; fresh thalli not or only little fragrant when crushed; terminal cells of photosynthetic filaments under pores not elongate and pyriform, but rounded on the free end; carpocephalum cruciate at maturity; gemma-receptacles crescent-shaped, usually present on some thalli of a population. . . . . **Lunularia**
8. Archegoniophores arising from the dorsal thallus surface behind the apex; antheridia scattered (not in a defined receptacle) in an elongate band on the dorsal thallus surface, with conspicuously elongate ostioles; ventral scales without marginal slime-hairs. . . . . **Athalamia**
8. Archegoniophore arising from the apex of a main or short lateral branch; antheridia developing in a usually well-defined receptacle on the dorsal thallus surface, without conspicuously elongate ostioles; ventral scales with marginal slime-hairs. . . . . **9.**
9. Carpocephalum with a conspicuous whitish or purplish pseudoperianth, which is longitudinally split into 6 or more linear segments. . . . . **Asterella**
9. Carpocephalum without or with an inconspicuous pseudoperianth, but when present not split into segments. . . . . **10.**

10. Carpocephalum nearly circular in circumference when mature, slightly convex on the upper surface, and nearly flat below; thallus very thin when dry; air-chambers large and empty; ventral scales small or rudimentary. . . . . **Cryptomitrium**
10. Carpocephalum hemispherical or subconical when mature; thallus thin or thick when dry; air-chambers usually with many secondary partitions; ventral scales conspicuous. . . . . . **11.**
11. Carpocephalum distinctly lobed; lids of mature capsules falling away in fragments; pores in the dorsal epidermis surrounded by 3–5 concentric circles of cells. . . . . **Reboulia**
11. Carpocephalum not or little lobed; lids of mature capsules falling away intact; pores in the dorsal epidermis surrounded by 2–3 (seldom more) concentric circles of cells. . . . . . **Mannia**

II. Plants Lacking Sporophytes

1. Thalli with gemma-receptacles. . . . . **2.**
1. Thalli without gemma-receptacles. . . . . **3.**
2. Gemma-receptacles cup-shaped; dorsal epidermis with compound pores. . . . . . **Marchantia**
2. Gemma-receptacles crescent-shaped; dorsal epidermis with simple pores. . . . . **Lunularia**
3. Plants aquatic that float on or below the water surface, or become stranded on soil at the water's edge. . . . . **4.**
3. Plants clearly terrestrial. . . . . **5.**
4. Plants aquatic and **either** a) floating on the water surface with several rows of conspicuous, large, purplish ventral scales that are pendent in the water column; oil-cells present in the dorsal epidermis and ventral scales of both aquatic and stranded thalli; **or** b) plants stranded, large and grayish-green, thin and usually with a shiny dorsal surface when dry; ventral scales hyaline and usually difficult to locate because of the numerous rhizoids. . . . . **Ricciocarpos**
4. Plants aquatic and suspended in the water column; ventral scales of both aquatic and stranded thalli vestigial or inconspicuous and in a single median row (but can appear to be in two rows when bifid); oil-cells absent in the dorsal epidermis and ventral scales.. . . . . (some species of) **Riccia**
5. Photosynthetic tissue with narrow, vertical, finger-like air-channels. . (some species of) **Riccia**
5. Photosynthetic tissue with air-chambers in one or more layers. . . . . **6.**
6. Dorsal epidermis with compound pores (cut thallus cross-sections to determine). . . . . . **7.**
6. Dorsal epidermis with simple pores (cut thallus cross-sections to determine). . . . . **8.**
7. Ventral scales hyaline to slightly purplish, in 4–6 rows (2–3 rows on each side of the midrib), with scattered oil-cells; gemma-receptacles usually present. . . . . **Marchantia**
7. Ventral scales deep purplish-black, in 2 rows (1 row on each side of the midrib), without oil-cells; gemma-receptacles always absent. . . . . **Preissia**
8. Air-chambers in a single layer (view in thallus cross-section), photosynthetic filaments attached to the chamber floor. . . . . **9.**
8. Air-chambers in more than one layer (view in thallus cross-section), photosynthetic filaments absent from the air-chambers (the chambers may be subdivided by cell-plates or secondary walls). . . . . **11.**
9. Thalli mostly 1–2.5 cm long × 2–5 mm wide; ventral scales dark blackish-purple, with a lanceolate appendage. . . . . **Targionia**
9. Thalli 1.5–25 cm long × 5–22 mm wide; ventral scales hyaline to purplish, with semi-circular or reniform appendages. . . . . **10.**
10. Thalli large, 5–25 cm long × 5–22 mm wide; ventral thallus tissue with slime-canals; freshly collected plants usually fragrant when crushed; terminal cells of filaments under pores elongate, somewhat pyriform at their free-ends; gemma-receptacles lacking. . . . **Conocephalum**
10. Thalli medium sized, 1.5–4 cm long × 5–10 mm wide; ventral tissue without slime-canals; freshly collected plants not, or only little fragrant when crushed; terminal cells of filaments under pores rounded at their free-ends: crescent-shaped gemma-receptacles usually present. . . . . **Lunularia**
11. Epidermal pores poorly developed, inconspicuous; dorsal epidermis often disintegrating in older thallus parts, especially upon drying, giving the thallus a frothy or spongy appearance. . . . . (some species of) **Riccia**
11. Epidermal pores well-developed and conspicuous; dorsal epidermis remaining intact in older thallus parts and upon drying. . . . . **12.**
12. Thallus wing with a thin, often undulating surface; dorsal epidermal cells with many chloroplasts; ventral scales small and inconspicuous or fragile and lacking; oil-cells lacking in the dorsal epidermis. . . . . **Cryptomitrium**

12. Thallus wing thin or thick, often firm and somewhat leathery, but not undulating; dorsal epidermal cells not richly chlorophyllose; ventral scales conspicuous and persistent; oil-cells usually present in the dorsal epidermis. . . . . **13.**
13. Thallus sparingly dichotomously branched, often appearing long and strap-shaped, branching generally lateral, of ventral origin; antheridia and/or archegonia on short lateral branches of ventral origin (look for short lateral branches on dry plants). (Dry thalli of *Targionia* occasionally fit this description, but key out earlier because they have air-chambers in a single narrow layer with photosynthetic filaments attached to the floor.) . . . . **14.**
13. Thallus frequently dichotomously branched, seldom appearing long and strap-shaped; antheridia and archegonia on main thallus branches. . . . . **16.**
14. Ventral scales with 2–3 hyaline appendages visible at the thallus apex; female branches with a conspicuous apical tuft of hyaline scale appendages; living plants of some populations fragrant, other populations not fragrant; plants of higher elevations, mostly above 1450 m. . . . . **Mannia fragrans**
14. Ventral scales with 1–2 purple or reddish-purple appendages usually not visible at the thallus apex; female branches without an apical tuft of scale appendages; living plants of most species not aromatic; plants of lower elevations, mostly below 1400 m. . . . . **15.**
15. Ventral scales with 1 (occasionally 2) appendages that usually do not extend beyond the thallus margin; archegonia and antheridia on short lateral branches of ventral origin; oil cells of ventral scales reddish in color. . . . . **Asterella bolanderi**
15. Ventral scales with 1–2 appendages that often extend beyond the thallus margin, but never forming an apical tuft at the thallus apex; archegonia on short lateral branches of ventral origin and antheridia on the dorsal surface of main branches; oil-cells of ventral scales hyaline. . . . . **Mannia californica**
16. Ventral scales in 2 or more irregular rows with the scale apex conspicuous and appendage-like (not constricted at the base from the main scale body), and the scale appendages usually conspicuously projecting apically and laterally beyond the thallus margin; ventral scales without oil-cells and 1-celled marginal slime-hairs. . . . . **Athalamia**
16. Ventral scales in 2 definite rows with the scale apex bearing 2 or more appendages that extend only little beyond the thallus margin; ventral scales with oil-cells and 1-celled marginal slime-hairs. . . . . **17.**
17. Ventral scales each with 2–4 appendages (look at several scales before deciding). . . . . **18.**
17. Ventral scales each with 1–2 appendages (look at several scales before deciding). . . . . **19.**
18. Dorsal epidermis roughened with elevated distinct pores and visible underlying areolation; thallus lateral margins entire (not scalloped or crenulate); ventral scales each with 2–4 appendages (look at several scales). . . . . **Asterella californica**
18. Dorsal epidermis smooth with only slightly elevated indistinct pores and indistinct underlying areolation; thallus lateral margins usually distinctly scalloped to crenulate; ventral scales each with 2 (seldom 3) appendages (look at several scales).. . . . . **Reboulia hemisphaerica**
19. Dorsal epidermis with a few, scattered oil-cells; ventral scales with 1 (rarely 2) appendages; plants of higher elevations, mostly above 1000 m. **Asterellagracilis**
19. Dorsal epidermis without oil-cells; ventral scales with 1–2 appendages; plants of lower elevation, mostly below 950 m. . . . . **Asterella palmeri**

Asterella P. Beauv. 1805
(Aytoniaceae)

This genus is separated from the other genera of complex thalloid liverworts by a) the presence of conspicuous pseudoperianths pendent from the lower surface of carpocephala, and b) pseudoperianths that are longitudinally divided into 6–14 narrow lanceolate segments.

Four species are confirmed for California.

Species Key

1. Thallus mostly with lateral branching of ventral origin; antheridia developing on the dorsal surface of a short lateral branch of ventral origin; archegoniophore developing at the apex of a short lateral branch of ventral origin. . . . . **A. bolanderi**
1. Thallus usually dichotomously branched; antheridia developing on the dorsal surface of a main branch; archegoniophore developing at the apex of a main branch (**note:** In *A.*

californica, the archegoniophore can appear to be lateral because of the continued growth of non-reproductive branches). . . . . **2.**

2. Plants dioicous; carpocephalum strongly lobed; filiform scales present at the apex of the archegoniophore; thallus air-chambers subdivided by secondary wall partitions; spore coat with fine areolation giving the spore a frothy appearance under the compound microscope. . . . . **A. californica**

2. Plants paroicous; carpocephalum little or not lobed; filiform scales absent at the apex of the archegoniophore; thallus air-chambers not, or only incompletely, subdivided by secondary wall partitions; spore coat without fine areolation and without a frothy appearance under the compound microscope. . . . . **3.**

3. Carpocephalum hemispherical evenly rounded in side view; pseudoperianth segment tips usually free at maturity; spores yellow to yellow-brown, 58–82 µm in diameter. . . . **A. gracilis**

3. Carpocephalum conspicuously conic in side view; pseudoperianth segment tips remain attached at maturity; spores dark brown to nearly black, 65–93 µm in diameter. . . . **A. palmeri**

Asterella bolanderi, A. californica and *A. palmeri* usually occur in summer-dry habitats of lower elevation and can occur in close proximity. *Asterella gracilis* generally occurs in damper, slower-to-dry habitats of higher elevation.

Excluded. Asterella saccata (Wahlenb.) A. Evans. Based on *Howell 704* (CAS), Sutliffe (1947) reported the presence of this species from the high Sierra Nevada of Inyo County. Examination of the *Howell 704* during this study, however, located the presence of a female thallus with archegonia in a pit-like depression on the dorsal surface of the thallus midrib, behind the apex. In addition, the morphology and structure of plants in *Howell 704* are consistent with *Athalamia hyalina*. No herbarium collection examined in the present study confirmed the presence of *A. saccata* in California.

Asterella bolanderi (Austin) Underw.

Distinctive features. With reproductive plants, look for a) on the same thallus, antheridia and archegonia on separate short lateral branches of ventral origin, b) archegoniophore with a few filiform scales on the stalk and at the apex, but none at the base, c) a strongly lobed carpocephalum in both living and dry plants, d) 10–16 whitish to purplish pseudoperianth segments that remain attached at sporophyte maturity, and e) yellowish-brown spores, 75–105 µm in diameter with a coarsely areolate distal face, the areolae 12–20 µm wide. Sporophytes mature late March through mid-June.

With vegetative plants, look for a) relatively long, sparingly dichotomously branched, strap-shaped thalli, b) mainly lateral branching of ventral origin, c) living thalli 1.5–4.5 mm wide, with a green dorsal surface and margins that turn purplish with age, d) dorsal epidermal cells with no or small trigones, e) margins of dry thalli usually very strongly incurved and nearly tubular, exposing the blackish-purple ventral surface, f) usually reddish-purple ventral scales, mostly with 1 hyaline to purplish appendage that usually does not extend beyond the thallus margin or apex, and g) oil-cells of ventral scales reddish in color.

Separation. The a) sparingly dichotomously branched, relatively long, strap-shaped main branches, b) location of both antheridia and archegonia on separate lateral branches of ventral origin, and c) spore markings, readily separate this species from others in the genus and most other complex thalloid liverworts. Vegetative plants can be confused with *Mannia californica* and *Targionia*. However, as seen in a thallus cross-section, *Targionia* has the photosynthetic tissue in a single thin layer with photosynthetic filaments attached to the chamber floor, unlike both *A. bolanderi* and *M. californica*. The latter two genera are in the same family (Aytoniaceae) and both have generally similar vegetative morphology and anatomy. See *M. californica* for separation from that species.

Illustrations. Frye and Clark 1937; Howe 1899; Schuster 1992b.

Habitat. Exposed to lightly-shaded summer-dry areas. Soil of meadows, and of creek-, road- and ravine-banks, soil around rock outcrops, open areas in chaparral and woodlands. Elevation usually below 1300 m, but occasionally up to 1550 m.

Distribution. Asterella bolanderi is endemic to southwestern Oregon and California. Calif. Geographic Regions: **CC**: Monterey Co. *Doyle 11354* (UC), **CR**: Tehama Co. *Doyle 8594* (UC), **KR**: Shasta Co. *Doyle 9125* (UC), **NC**: Mendocino Co. *Doyle 10416* (UC), **SC**: Riverside Co. *Doyle 7326* (UC), **SN**: Nevada Co. *Doyle 8498* (UC).

Asterella californica (Hampe) Underw.

Caution. This is the most common and widespread species of *Asterella* in California. Non-reproductive, vegetative plants can be variable in color and growth characteristics, and occasionally are challenging to identify. The dorsal surface of plants collected early following the onset of winter rains, or from dimly-lit and/or wet habitats (e.g., wet shaded underhangs of cliff faces and boulders, and shaded streambanks and seepages), can be nearly uniformly green with little or no yellowish-brown to brown to purplish-black coloration of the lateral margins, and with little or no purplish-black coloration of the ventral thallus surface or scales. Moreover, the lateral margins of these plants often do not incurve when dry. The appearance of these plants contrasts markedly with plants collected later in the year from the same area, or from plants that grow in more exposed habitats; these plants generally have yellowish-brown to brown to purplish-black lateral margins and purplish-black ventral surfaces and scales. When dry, the margins of these "typical" plants usually are strongly incurved over the photosynthetic tissue, often with only the dark ventral surface and scales exposed to the environment.

Distinctive features. This is the only dioicous species of this genus in California. With reproductive plants, look for a) separate female and male plants, b) antheridia clustered in distinctive non-stalked receptacles on the dorsal thallus surface of main branches (mature receptacles of plants in exposed habitats usually are purplish and slightly elevated above the thallus surface, and often have small scales around the receptacle margin; plants from wet or dimly-lit habitats often have antheridia in a slightly raised single or double row that lacks purplish coloration and scales), c) a cluster of filiform hyaline scales at the archegoniophore apex and none at the base, d) a strongly 3–4 (occasionally 5) lobed carpocephalum, with pseudoperianths directed obliquely to nearly horizontally outward, e) hyaline pseudoperianths with 12 or more segments, the segment tips remain attached at sporophyte maturity, f) distinctive yellow spores, 95–125 μm in diameter, the distal face usually with broad, rounded folds/ridges that occasionally form one or more large areolae, and g) finely areolate surface texture of both distal and proximal faces, which give the spore a frothy appearance with the compound microscope. Sporophytes mature early February through late May.

With vegetative plants, look for a) frequently dichotomously branched thalli, the branches 0.9–2.3 cm long and 5–10 mm wide and b) hyaline ventral scales usually with 2–4 appendages.

Separation. This species is readily separated from others of the genus by its yellow, frothy-appearing spores. Occasionally, however, non-reproductive plants of *A. californica* occuring in damp shaded habitats have lateral margins that are yellowish-brown to brown and remain flat when dried. Vegetative plants of this species have been confused with the related species, *Reboulia hemisphaerica.* The two species can be separated by a) lateral thallus margins entire in *A. californica* (vs. distinctly scalloped to crenulate lateral margins in *R. hemispherica*) and b) *A. californica* has 2–4 scale appendages that are subulate with acute apices (vs. usually only 2 scale appendages that are linear with acute apices).

Male plants of *A. californica* from exposed habitats and with mature antheridial receptacles are distinctive and should not be confused with male plants of other complex thalloid liverworts. However, male plants from wet or dimly lit habitats occasionally have antheridia in only one or two rows and only slightly elevated on poorly differentiated receptacles. These plants superficially can be confused with male plants of *Athalamia hyalina.* Look at the ventral scales: the ventral scale of *Asterella californica* has 2–4 appendages that are sharply differentiated from the main scale, whereas the ventral scale of *Athalamia hyalina* has a single, long triangular "appendage" that is not constricted at the base or sharply differentiated from the main scale.

Illustrations. Frye and Clark 1937; Howe 1899.

Habitat. Diverse exposed to lightly shaded areas that dry soon after cessation of spring rains, such as open areas in chaparral and oak woodlands, and on rock and sandstone outcrops, ravine banks, and cliffs. Elevation mostly from near sea-level to 1200 m, but occasionally up to 2000 m.

Distribution. Asterella californica occurs in southwest Oregon, California, Arizona and Mexico (incl. Guadalupe Island). Calif. Geographic Regions: **CC**: San Mateo Co. *Whittemore 4407* (CAS), **CR**: Tehama Co. *Doyle 8624* (UC), **DSon**: San Diego Co. *Doyle 11274* (UC), **KR**: Trinity Co. *Doyle 5821* (UC), **NC**: Colusa Co. *Kellman 2731* (CAS), **SC**: San Diego Co. *Doyle 9902* (UC), **SN**: Tulare Co. *Shevock 12983* (CAS).

Asterella gracilis (F. Weber) Underw.

Because of a taxonomic mixup, this species is listed as *A. ludwigii* (Schwaegr.) Underw. in older publications (e.g., Frye and Clark 1937).

Distinctive features. With reproductive plants, look for a) archegoniophores, often reddish near the base, at the apices of main branches, b) antheridial receptacles sessile in a small, often poorly defined, purplish cluster either (1) posterior to the archegoniophore or (2) on a separate branch, c) archegoniophore lacking an apical tuft of scales and scales inconspicuous or absent at the base, d) carpocephala of living plants nearly hemispherical and little lobed (the lobing is more pronounced in dry carpocephala), and with pseudoperianths directed obliquely or nearly vertically downward, e) hyaline or slightly reddish-purple pseudoperianths, each usually with 6–8 segments; the segment tips usually are free at sporophyte maturity, f) yellow to yellowish-brown spores, 58–82 µm in diameter, the distal spore face with rounded sinuous ridges that intersect and usually form shallow areolae 8–16 µm wide. Sporophytes mature late April through August.

With vegetative plants, look for a) often slightly fragrant living plants, b) usually dichotomously branched thalli, 0.5–1.5 cm long and 1–3 mm wide, c) green dorsal thallus surface, often with reddish lateral margins, and (usually) shiny reddish-purple ventral surface and scales, d) dorsal epidermis with a few, scattered oil-cells, and e) ventral scales mostly with a single appendage.

Separation. Details of spore markings (yellow to yellowish-brown and non-frothy) easily separate this species from others in the genus. In addition, the combination of a) slight fragrance of living plants, b) frequently dichotomously branched, c) usual reddish coloration of thallus margins, d) shiny reddish-purple of the ventral surface and scales, and e) a plant of higher elevation can be used to separate vegetative plants of *A. gracilis* from the other species in the genus.

Illustrations. Damsholt 2002; Frye and Clark 1937 (as *A. ludwigii*); Schofield 2002; Schuster, 1992b.

Habitat. A species of slow-to-dry, higher elevations. Damp soil of seepages, creek and lake banks, cliff recesses, and rock outcrops; splash of cascades and waterfalls. Elevation usually above 1500 m, but down to 550 m in Plumas Co.

Distribution. *Asterella gracilis* occurs in Europe, Asia, and North America. Calif. Geographic Regions: **CR**: Shasta Co. *Doyle 9887* (UC), **KR**: Trinity Co. *Doyle 4627* (UC), **MP**: Modoc Co. *Doyle 2889* (UC), **NC**: Humboldt Co. *Norris 50159* (UC), **SN**: Mariposa Co. *Shevock 18491* (CAS).

Asterella palmeri (Austin) Underw.

This species, like the others in the genus, has spores with species-specific markings. Study immature spores of *A. palmeri*, because mature spores are opaque and the markings can be difficult to discern.

Distinctive features. With reproductive plants, look for a) antheridia in a small irregular receptacle usually posterior to the archegoniophore, b) at the apex of a main branch, an archegoniophore that lacks basal and apical scales, c) in living plants, a carpocephalum nearly conical and scarcely lobed with the pseudoperianths directed nearly vertically downward; in dry plants, the top of the carpocephalum shrinks considerably and the pseudoperianths usually are directed obliquely outward, d) pseudoperianths with 8–12 hyaline segments, the tips of which remain attached at maturity, e) dark-brown to nearly black mature spores 65–93 µm in diameter; the distal spore face usually with short, rounded and tightly spaced ridges. Sporophytes mature late February through early May.

With vegetative plants, look for a) usually dichotomously branched thalli, 0.5–1 cm long and 2–5 mm wide, b) brownish-black to purplish thallus margins usually strongly incurved in dry plants, c) absence of oil-cells in the dorsal epidermis, and d) ventral scales with 1–2 appendages.

Separation. The dark brown, nearly opaque spores separate this species from others in the genus. Also distinctive in living plants is the conical carpocephalum with pseudoperianths directed nearly vertically downward.

Illustrations. Frye and Clark 1937; Howe 1899.

Habitat. Exposed to lightly shaded summer-dry soil; usually on gentle to steep slopes around chaparral, *Quercus* and *Pinus*. Elevation usually below 950 m, but up to 1250 m in the southern Sierra Nevada.

Distribution. *Asterella palmeri* is restricted in distribution to California and northern Baja California, Mexico. Calif. Geographic Regions: **CC**: Monterey Co. *Doyle 8115* (UC), **NC**: Sonoma Co. *Baker 2* (UC), **SC**: Riverside Co. *Doyle 7256* (UC), **SN**: Kern Co. *Laeger 2553* (CAS).

Athalamia Falc. 1851
(Cleveaceae)

The presence of pit-like depressions in the midrib tissue of the dorsal thallus surface of female plants is a distinctive feature of this genus. These depressions contain archegonia, and, following fertilization, the archegoniophore develops in these depressions.

A single species in California.

Athalamia hyalina (Sommerf.) S. Hatt.

Distinctive features. With reproductive plants, look for a) antheridia, with conspicuous, elongate hyaline ostioles, in an elongate band on the dorsal midrib region of male plants, b) one or more circular or elongate pit-like depressions with projecting white lanceolate scales on the dorsal midrib region of female plants; post-fertilization, the scales are elevated at the apex of the archegoniophore, c) the archegoniophore arising from the midrib dorsal surface well behind the thallus apex, and d) distinctive orange- to reddish-brown spores, 45–64 μm in diameter, with numerous, prominent hemispherical bumps or blisters on the distal spore face. Sporophytes of plants below 1820 m generally mature mid-March through May; above 1820 m from late May through September.

With vegetative plants, look for a) dull- to gray-green thalli 0.5–1.5 cm long and 2.5–5.5 mm wide, b) hyaline or purplish appendage-like apices of ventral scales that often form conspicuous apical clusters and also usually extend beyond the lateral thallus margins, c) simple epidermal pores with a single (sometimes indistinct) circle of cells that sometimes appear stellate in surface view because of wall thickening on the radial cell walls (**note**: cells around the pores of plants collected early in the growing season or from moist habitats can lack the thickened radial walls), and d) ventral scales in 2 to several irregular rows and which lack oil-cells and 1-celled slime filaments.

Separation. Pit-like chambers in the midrib region of the dorsal surface of female thalli separate *A. hyalina* from other California complex thalloid liverworts. Search field populations for thalli with young or last year's pit-like depressions. Male plants also are distinctive—antheridia a) are in an elongate band in the midrib region of the dorsal surface, b) have conspicuous, elongate hyaline ostioles, and c) are not in a well-defined receptacle. See *Asterella californica* for separation of male plants of that species from *Athalamia hyalina*.

Vegetative plants can be separated by the combination of a) presence of conspicuous hyaline or purplish ventral scale appendages that usually extend beyond the thallus apex and lateral margin and b) pores of air-chambers surrounded by a single circle of cells.

Illustrations. Damsholt 2002; Frye and Clark 1937; Schofield 2002; Schuster 1992b.

Habitat. Damp and slow-to-dry soil around granite rocks, and limestone, sandstone, granitic and metamorphic outcrops; margin of drainages and steep hillsides. Elevation from near sea-level to 3820 m.

Distribution. Athalamia hyalina occurs in Europe, Asia, and North America. Calif. Geographic Regions: **CC**: Monterey Co. *Doyle 10910* (UC), **DSon**: San Diego Co. *Doyle 7078* (UC), **KR**: Trinity Co. *Doyle 6621* (UC), **MP**: Modoc Co. *Doyle 7492* (UC), **SC**: Los Angeles Co. *Doyle 10366* (UC), **SN**: Inyo Co. *Doyle 6650* (UC).

Conocephalum Hill 1780
(Conocephalaceae)

The following combination of characteristics separates this genus from other complex thalloid liverworts: a) large size of the thallus (6 to 25 cm long), b) air-chambers in a single layer and with simple pores, c) elongate (beaked) terminal cells of photosynthetic filaments under the pores, d) male receptacles terminal on very short branches, and e) spores germinate and become multicellular prior to discharge from the capsule.

The number of species in the genus and the name of the species in California is uncertain. Until recently, *Conocephalum conicum* was considered to be the name of the species in California. However, Szweykowski et al. (2005) restricted *C. conicum* to Europe and placed collections from the U.S.A. and India in a new species, *C. salebrosum* Szweyk. et al. They also reported that there are six cryptic species in *C. conicum*. The morphology of California specimens examined in this study fit *C. salebrosum*. However, Forrest et al (2006) have determined that although Illinois specimens are morphologically like *C. salebrosum*, they are very distinct from this species in molecular sequence data. They recommend that the cryptic species diversity within *C. conicum* s.l. needs further investigation. In the

present publication, we use *C. conicum* s.l. and look forward to the resolution of this taxonomic question.

Conocephalum conicum (L.) Dumort. *s. l.*

Distinctive features. Most populations will be vegetative or without sporophytes. The simplest way to identify *C. conicum* s. l. in the field is to crush a small bit of the fresh thallus—released will be a strong to weak musty or mushroomy aroma. With dry plants, look for a) large thalli, 6–25 cm long and 6–22 mm wide, b) simple pores and air-chambers in a single, thin layer with photosynthetic filaments attached to the chamber floor, c) terminal cells of filaments immediately below the pores conspicuously elongate (beaked) and with few or no chloroplasts, d) mucilage cells in the ventral thallus tissue, e) male plants with violet to purple oval, circular or crescentic antheridial receptacles sessile on the dorsal surface of very short lateral branches, f) archegoniophores at the apices of main branches, g) a strongly conical carpocephalum with 6–9 very short lobes, and h) spores 72–93 μm in diameter, with thin light-brown walls; the spores become multicellular through cell divisions prior to spore discharge. Sporophytes mature late January through April.

Separation. Conocephalum conicum s. l. occasionally grows in proximity to *Marchantia* and *Lunularia*. It is separated from *Marchantia* by the presence of simple dorsal epidermal pores (vs. compound pores), and from both *Marchantia* and *Lunularia* by the absence of gemma-receptacles.

Illustrations. Damsholt 2002; Frye and Clark 1937; Paton 1999; Schofield 2002; Schuster 1992b.

Habitat. Shaded sites; compacted soil, rocks and walls of ditches, creeks, rivers, and seepages. Usually close to water where it is seasonally inundated and there is elevated humidity during summer months. Elevation from near sea-level to 2520 m.

Distribution. Conocephalum conicum s. l. occurs in Europe, Asia, North Africa, and North America. Calif. Geographic Regions: **CC**: Monterey Co. *Doyle 6147* (sporophytes) (UC), **KR**: Trinity Co. *Doyle 5810* (UC), **MP**: Modoc Co. *Doyle 6692* (UC), **NC**: Humboldt Co. *Doyle 7683* (UC), **SN**: Mono Co. *Doyle 6724* (UC).

Cryptomitrium Austin ex Underw. 1883
(Aytoniaceae)

Distinctive features of this complex thalloid liverworts are: a) an unlobed, nearly circular carpocephalum that is only slightly convex on the upper surface and nearly flat on the lower, b) a thin thallus with a somewhat shiny dorsal surface (especially on dry plants), and c) thin-walled dorsal epidermal cells that contain numerous chloroplasts.

A monotypic genus.

Cryptomitrium tenerum (Hook.) Austin ex Underw.

Distinctive features. With reproductive plants, look for a) sessile antheridia, in 1–2 rows immediately behind the archegoniophore on the dorsal thallus surface, b) archegoniophores at the apex of main branches, c) when mature, a carpocephalum that is circular to discoidal in outline, and bears 3–7 sporophytes, d) in side view, the upper surface of the carpocephalum is slightly convex, and the lower surface is nearly flat, and e) light to dark brown spores, 45–60 μm in diameter, the distal spore face with irregular areolae. Sporophytes mature late February through March.

With vegetative plants, look for a) a thin thallus; the dorsal surface of dry plants often appears fragile (not firm or leathery), b) often somewhat undulate, but not crenulate, lateral thallus margins that do not or only little incurve when dry, c) yellowish-brown older thallus areas, d) dorsal epidermal cells with numerous chloroplasts and without oil-cells, e) large air-chambers sparingly divided by supplementary wall partitions, and f) small ventral scales in 2 rows, each with 2 filiform appendages; the scales sometimes fragmentary.

Separation. This species should easily be separated from other complex thalloid liverworts by a) the unlobed carpocephalum with a low, rounded dome on the upper surface and a flat lower surface, b) the relatively thin vegetative thallus often with an undulate lateral wing that usually does not incurve when dry and c) the large number of chloroplasts in cells of the dorsal epidermis.

Illustrations. Frye and Clark 1937; Howe 1899; Schofield 2002.

Habitat. Usually calcareous substrates. Damp, mostly dimly-lit and somewhat humid habitats. Soil of rock outcrops, steep hillsides, recesses in cliffs and creek banks; usually shaded by chaparral, oaks, rock overhangs or narrow canyon walls. Elevation from 45 to 1200 m; mostly below 800 m.

Distribution. Cryptomitrium tenerum occurs in southwest Oregon (David Wagner, personal communication), south to Central and South America. Calif. Geographic Regions: **CC**: Santa Cruz Co. *Doyle 6105* (UC), **CR**: Tehama Co. *Doyle 5767* (UC), **NC**: Napa Co. *Howell 476* (CAS), **SC**: Santa Barbara Co. *Doyle 10345* (UC), **SN**: Tulare Co. *Shevock 17022* (CAS).

Lunularia Adans. 1763
(Lunulariaceae)

The occurrence of crescent-shaped gemma-receptacles on the dorsal thallus surface is a definitive feature of this genus.
A monotypic genus.

Lunularia cruciata (L.) Lindb.

Distinctive features. Distinctive are crescent-shaped gemma-receptacles on the thallus dorsal surface. These receptacles generally are present on at least a few thalli in most populations. Also look for a) light- to gray- to yellow-green thalli, sometimes browning with age, 1.5–4 cm long and 5–10 mm wide; the thallus margins often incurve when dry, b) air-chambers with simple pores and in a thin single layer, c) photosynthetic filaments 3–4 cells long, the terminal cells under the pores densely chlorophyllose and about the same size as the subtending cells, and d) hyaline to light-brown ventral scales in two rows, each scale with 1 semicircular appendage.

Sporophytes are rare in this dioicous species, and, in California, known only from Marin County (*Proskauer s.n.* [dated 1953 and 1962] [UC]). From November to June, look for a) antheridia in a clearly defined, slightly raised purplish receptacle with raised margins on the dorsal thallus surface of very short branches, b) female plants with conspicuous apical clusters of hyaline scales at the apices of short, lateral branches that bear archegonia, c) a carpocephalum with (usually) 4 finger-like, nearly horizontal (cruciate) lobes and capsules that dehisce by 4 valves.

Separation. Lunularia is a distinctive plant and easily separated from other complex thalloid liverworts when crescent-shaped gemma-receptacles are present. Plants without gemma-receptacles have been confused with small, non-gemmiferous thalli of *Marchantia*, with small thalli of *Conocephalum* and with *Reboulia*. *Lunularia* is separated a) from *Marchantia* by the presence of simple thallus pores (vs. compound pores), b) from *Conocephalum* by its smaller thallus size (1.5–4 cm long × 5–10 mm wide vs. 6–25 cm long and 6–22 mm wide) and the lack of a distinctive aroma from crushed living thalli, and c) from *Reboulia* by air-chambers in a single layer (vs. in more than one layer).

Illustrations. Damsholt 2002; Frye and Clark 1937; Schofield 2002; Schuster 1992b.

Habitat. Soil of shaded drainages, and creek and river banks; usually occurs higher on banks than does *Marchantia* and *Conocephalum*. It also occurs under and near chaparral of gentle-sloping hills (e.g., off the Edwards Trail, of the Joseph D. Grant Santa Clara County Park). Elevation from 20 to 1800 m; mostly below 650 m.

Distribution. Lunularia (like *Marchantia*) is a greenhouse, nursery-yard, and garden weed, where it reproduces asexually and disperses by means of multicellular gemmae. Most researchers consider *Lunularia cruciata* to be a native of the Mediterranean region; it occurs in Europe, Asia, Africa, North, Central, and South America, New Zealand, and Australia. Calif. Geographic Regions: **CC**: San Mateo Co. *Doyle 9931* (UC), **CR**: Tehama Co. *Doyle 8588* (UC), **NC**: Marin Co. *Proskauer s.n.* (1 Dec. 1953 & 10 Jan. 1962, both collections with sporophytes) (UC), **SC**: San Diego Co. *C. Wagner 932* (UC), **SN**: Inyo *Shevock 15283* (CAS).

Mannia Opiz 1829
(Aytoniaceae)

Species in this genus have a) a thallus dorsal epidermis with simple pores, each surrounded by 1–3 concentric circles of cells, b) air-chambers in more than one layer, the chambers sparingly divided by supplementary wall partitions, c) oil-cells present in both the dorsal epidermis and ventral parenchyma

tissue, d) antheridia sessile on the dorsal thallus surface, e) sporophytes elevated on archegoniophores, and f) no pseudoperianth around each sporophyte.

Two species in California.

Species Key

1. Ventral scales with 2–3 hyaline appendages usually forming a conspicuous cluster at the apex of female branches; archegoniophores developing at the apex of a main branch or large ventral branch, with a conspicuous basal and apical cluster of hyaline scales; spores yellow to yellow-brown. . . . . **M. fragrans**
1. Ventral scales with 1–2 usually purplish appendages never forming a conspicuous apical cluster; archegoniophores usually developing at the apex of a short branch of ventral origin, without a basal or apical cluster of scales; spores reddish- to dark purple. . . . **M. californica**

Mannia californica (Gottsche ex Underw.) L. C. Wheeler

Distinctive features. With reproductive plants, look for a) antheridia in an ill-defined group on a main branch, b) archegoniophores at apices of short, lateral branches of ventral origin and lacking basal and apical clusters of scales, c) hemispherical, obscurely lobed carpocephala, d) reddish- to dark-purple spores, 69–82 µm in diameter; the distal spore face with irregular large bumps, folds and ridges that do not intersect and form areolae, e) a flattened proximal spore face with facets between arms of the triradiate ridge with small, low bumps and thin ridges, with the ridges often intersecting to form small areolae, and f) the surface texture of both distal and proximal faces roughened by very small, rounded papillae and granules. Sporophytes mostly mature from March through May.

With vegetative plants, look for a) plants with a grayish-green dorsal surface and brownish lateral margins, b) strongly incurved (sometimes tubular) thallus margins in dry plants, c) air-chambers subdivided by many supplementary walls, d) medium to large, concave-sided trigones in dorsal epidermal cells, e) purplish black ventral surface and scales, f) ventral scales with 1–2 accuminate, usually purplish appendages that do not form a dense apical cluster, and g) ventral scales with hyaline oil-cells.

Separation. Mature, dry vegetative plants of *M. californica* and *Asterella bolanderi* often have strongly incurved margins that appear tubular and blackish. For easy separation, cut a thin section with a razor blade parallel to the dorsal epidermis; epidermal cells of *M. californica* have medium to large trigones (vs. none or small trigones in *A. bolanderi*). Occasionally, robust dry thalli of *Targionia* (especially from southern California) also are tubular and blackish. Cut a thallus cross-section with a razor blade. *M. californica* has an air-chamber system with many supplementary wall partitions but no photosynthetic filaments (vs. air-chambers in a thin single layer with photosynthetic filaments in *Targionia*).

Illustrations. Howe 1899; Schuster 1992b.

Habitat. Not common, but occasionally it forms large local populations. Exposed or shaded, somewhat slow to dry, summer-dry soil around rocks of hillsides and cliffs; and often under chaparral and *Quercus*. Elevation from 130 to 1800 m, but generally below 1300 m.

Distribution. Mannia californica is known only from two widely disjunct areas in the United States: 1) Arkansas and North Carolina (Ozarks and Appalachian Mts.) and 2) Arizona and California. Calif. Geographic Regions: **CC**: Monterey Co. *Doyle 192* (UC), **DMoj**: San Bernardino Co. *Laeger 2479* (CAS), **NC**: Solano Co. *Doyle 860* (UC), **SC**: San Diego Co. *Doyle 7171* (UC), **SN**: Tulare Co. *Shevock 17021* (CAS).

Mannia fragrans (Balb.) Frye and L. Clark

The species name *fragrans* refers to the fragrant aroma of fresh thalli. In the field, occasionally the nose can lead the eye to a nearby population. **However, do not use aroma alone as the only clue to the presence or identification of this species because not all populations are fragrant.**

Distinctive features. Sporophytes usually mature soon after liberation from snow cover. With reproductive plants, look for a) antheridia in a defined receptacle on the dorsal thallus surface, b) a cluster of hyaline scales at the apices of branches with archegonia, c) clusters of white scales at both the base and apex of archegoniophores (occasionally the archegoniophore elongates very little

before spore discharge), d) yellowish- to light-brown spores, mostly 58–84 µm in diameter; however, spores of plants along the trail to Long Gulch Lake, Siskiyou Co., *Doyle 5976* (UC), are smaller, ranging from 47–65 µm, e) prominent, thick rounded ridges that often intersect to form areolae on the distal face, and f) thinner ridges and smaller areolae on the proximal face. Sporophytes generally from mid-April to July.

With vegetative plants, look for a) plants often forming dense populations, b) green or whitish-green thallus dorsal surface and purplish lateral margins, c) deep purplish-black ventral surface and scales, d) cells of the dorsal epidermis with thick walls and large to bulging trigones, e) dark colored ventral scales usually with 2–3 hyaline appendages, and f) dry plants that appear blackish and tubular, with strongly incurved margins and conspicuous hyaline scale appendages.

Separation. With the archegoniophore at the thallus apex, and conspicuous clusters of hyaline scales at both its base and apex, reproductive plants of *M. fragrans* can hardly be confused with any other California liverwort. At times, however, vegetative plants can be confused with *Reboulia hemisphaerica* and *Asterella gracilis*. Dried plants of California populations of *R. hemisphaerica*, however, seldom are blackish or as tightly tubular, and they lack hyaline scale appendages. *Asterella gracilis* is separated from *M. fragrans* by its a) thin-walled epidermal cells with small or no trigones (vs. thick-walled epidermal cells with large to bulging trigones in *M. fragrans*), b) ventral scales usually with only one appendage (vs. usually 2–3 ventral scales in *M. fragrans*) and c) thallus lateral margins and ventral scales reddish (vs. purplish-black thallus margins and ventral scales). Tubular and blackish dried vegetative thalli of *M. fragrans* also can be confused with dry plants of both *Asterella bolanderi* and *Mannia californica*. However, *M. californica* and *A. bolanderi* do not have hyaline scale appendages that extend beyond the thallus margins and apices of female plants, and they are plants of lower elevations.

Illustrations. Damsholt 2002; Frye and Clark 1937; Schofield 2002; Schuster 1992b.

Habitat. Gravelly soil around rocks and outcrops; hillsides and banks of ephemeral creeks; often in exposed areas that dry soon after snow-melt. Elevation range from 1450 to 3650 m.

Distribution. Mannia fragrans occurs at higher elevations in Europe, Asia, and North America. Calif. Geographic Regions: **KR**: Siskiyou Co. *Shevock 25869* (CAS), **MP**: Modoc Co. *Doyle 7491* (UC), **SN**: Inyo Co. *Doyle 5899* (UC).

Marchantia L. 1753
(Marchantiaceae)

The presence of cup-shaped gemma-receptacles on the dorsal thallus surface is a definitive feature of this genus. Also look for a) compound pores in the dorsal epidermis, b) antheridiophores and archegoniophores, and c) carpocephala with finger-like rays.

A single species in Californica—*Marchantia polymorpha*. The high morphological variability of this species has resulted in description of some 50 species and infraspecific taxa (subspecies, varieties, forms, subforms). Schuster (1992b) and Damsholt (2002) separate *M. polymorpha* into three species; Paton (1999) uses three subspecies. In research that combined morphological studies and electrophoretic techniques, Bischler-Causse and Boisselier-Dubayle (1991) reported that electrophoretic patterns indicated the existence of three major and clearly distinct groups, which they considered to be subspecies. However, they reported difficulting in assigning individual samples to a subspecies based on morphological features alone. We also have found that many California specimens also are not assignable to a subspecies (or species of Damsholt and Schuster) only on morphological characters. Without experimental work (which is not practical), it is not possible to be totally sure to which subspecies your specimen belongs. Therefore, in this publication the species *M. polymorpha* is circumscribed in a broad sense (*sensu lato* or *s. l.*).

Marchantia polymorpha L. *s. l.*

Distinctive features. This dioicous species has large pale- to dark-green thalli, 5–10 mm wide and up to 10 cm or more long. Thalli usually are prostrate, but are ascending when growing among other bryophytes. The dorsal surface of some thalli have a strong, weak, interrupted or continuous dark line that extends over the midrib. Look for a) cup-shaped gemma-receptacles with lobed, fringed margins and which contain multicellular gemmae, that occur on the dorsal surface of at least some plants in most populations, b) compound dorsal epidermal pores that lead into air-chambers, c) air-chambers in a single thin layer that contain photosynthetic filaments, d) 4–6 rows (2 to 3 rows on each side of the midrib) of purple or hyaline ventral scales with oil-cells.

Sporophytes are not common although antheridiophores and archegoniophores occur from May to September. Look for a) the upper surface of the antheridiophore nearly circular in outline and with an upturned membranous margin, b) carpocephala usually with 7–11 prominent finger-like rays (resembling spokes of an umbrella), and c) small yellowish spores, 10–14 μm in diameter.

Separation. This is the only genus with circular, cup-shaped gemma-receptacles. Although *Marchantia* and *Preissia* both have compound pores in the gametophyte, *Preissia* lacks gemma-receptacles. Young or non-gemmiferous thalli of *Marchantia* are separated from *Preissia* by the presence of ventral scales in 4–6 rows (vs. ventral scales in only 2 rows in *Preissia*).

Illustrations. Damsholt 2002; Paton 1999; Schofield 2002; Schuster 1992b.

Habitat. This species often forms very large populations and occurs in diverse habitats: damp and wet places, occasionally submerged; on soil, rocks and organic matter near creeks, rivers, seepages, gardens (where it can be invasive), and burned-over areas (where it can be a pioneer species). Elevation from near sea-level to over 3600 m.

Distribution. Marchantia polymorpha is nearly world-wide in distribution. Like *Lunularia*, it often is a greenhouse, nursery-yard and garden weed. In California, it is a native plant, but its distribution is considered to have increased due to human activity. Calif. Geographic Regions: **CC**: Monterey Co. *Kellman 3356* (CAS), **CR**: Siskiyou Co. *Shevock 25877* (CAS), **KR**: Del Norte Co. *Doyle 7746* (UC), **MP**: Modoc Co. *Norris 108483* (UC), **NC**: Glenn Co. *Shevock 15878* (female plants) (UC), **SC**: San Diego Co. *Wiggins 2850* (UC), **SN**: Mono Co. *Doyle 10114* (female and male plants) (UC).

Preissia Corda 1829
(Marchantiaceae)

Preissia has compound pores in the dorsal epidermis that lead into air-chambers, and antheridia and sporophytes elevated on antheridiophores and archegoniophores, respectively. In addition, a) it lacks gemma-receptacles and gemma development, b) it has ventral scales in only two rows and each scale has a single subulate appendage, and c) its carpocephalum is lobed, but lacks finger-like rays.

A monotypic genus.

Preissia quadrata (Scop.) Nees

Distinctive features. With vegetative plants, look for a) dull- to gray-green thalli, 0.6–15 mm wide and 0.5–3 cm long, with lateral margins often becoming brownish- or reddish-purple with age, b) thallus margins of dry plants usually not or only little incurved, c) thin-walled dorsal epidermal cells without trigones, d) air-chambers with compound pores, in a thin single layer and with branched photosynthetic filaments, and e) purplish-black ventral scales in two rows, without oil-cells, and each scale with a single, subulate appendage.

California plants appear to be dioicous. From July thorugh September, look for a) male plants with antheridiophores and female plants with archegoniophores, b) a (usually) 4-lobed carpocephalum with quadrate low ridges on the upper surface, and c) angular brown spores 55–80 μm in diameter, with numerous wavy lamellae that occasionally form coarse areolae on the distal face.

Separation. Thalli of *Preissia* are about the same size and have similar secondary coloration as *Reboulia hemisphaerica*. *Preissia* is separated by a) compound thallus pores (vs. simple pores in *R. hemisphaerica*), b) ventral scales with a single appendage (vs. scales with 2–3 appendages), and c) antheridiophores (vs. sessile antheridia). *Preissia* might also be confused with young plants of *Marchantia polymorpha*—both have gametophytes with compound pores. *Preissia* can be separated by a) absence of gemma-receptacles (vs. gemma-receptacles present in *M. polymorpha*), b) ventral scales in 2 rows (vs. ventral scales in 4–6 rows), and c) a carpocephalum without finger-like rays (vs. a carpocephalum with finger-like rays).

Illustrations. Damsholt 2002; Frye and Clark 1937; Paton 1999; Schofield 2002; Schuster 1992b.

Habitat. Damp soil and rocks of shaded creek banks and seepages; splash of creeks and cascades; often under willow; places that remain damp for long periods of time following snow-melt. It occurs between 2600 to 3550 m in the central and southern Sierra Nevada, and above 1500 m in the Klamath Ranges.

Distribution. Preissia quadrata occurs in Europe, Asia, and North America. Calif. Geographic Regions: **KR**: Trinity Co. *Duell 1740.11-1g.* (ABSH), **SN**: Tulare Co. *Doyle 7849A* (female) & *7849B* (male) (UC).

Reboulia Raddi 1818
(Aytoniaceae)

Distinctive characteristics of this genus include a) simple pores of the dorsal epidermis surrounded by 4–6 concentric circles of cells b) ventral scale appendages with 2–3 filiform appendages and b) conspicuous filiform scales at the base and apex of the archegoniophore.
A single species in California.

Reboulia hemisphaerica (L.) Raddi

Distinctive features. The firm, somewhat leathery, dull light-green thallus is 4–9 mm wide × 1.5–4 cm long. With vegetative plants, look for a) thalli usually with scalloped to crenulate lateral margins that are brownish to brownish-purple, b) often thin and somewhat parchment-like dry thallus margins, c) bulging trigones in mature dorsal epidermal cells, d) simple pores in the dorsal epidermis with 4–6 concentric circles of cells, the pores only slightly elevated, and e) purplish ventral scales, often with whitish margins, and with scattered hyaline oil-cells, marginal 1-celled slime-hairs, and usually 2–3 filiform appendages on each scale.
With reproductive plants, look for a) antheridia in sessile, mostly reniform, receptacles bordered by small purplish scales, b) archegoniophores with basal and apical filiform scales, and c) yellow to yellowish-brown spores 65–80 µm in diameter; the distal spore face with a few large areolae, 16–20 µm wide. Sporophytes mature late March through May.

Separation. Vegetative plants of *R. hemisphaerica* have a superficial resemblance to *Preissia quadrata*. *Reboulia hemisphaerica* is separated from *P. quadrata* by a) vegetative thallus with simple thallus pores (vs. compound pores *P. quadrata*), b) dorsal epidermal cells with bulging trigones (vs. dorsal epidermal cells with no trigones) and c) ventral scales with 2–3 filiform appendages (vs. ventral scales with only 1 subulate appendage). For separation from *Asterella californica*, see discussion under that species.

Illustrations. Damsholt 2002; Frye and Clark 1937; Schofield 2002; Schuster 1992b.

Habitat. Soil on small ledges and in channels of steep metamorphic rock outcrops; soil of hillsides. Elevation below 900 m.

Distribution. Reboulia hemisphaerica is widespread in the temperate and warmer regions of both the Northern and Southern Hemisphere. Its known distribution in California consists of three disjunct populations: two sites on the western slope of the Sierra Nevada and one in the City of San Francisco (at Laguna de la Puerca, now known as Pine Lake, near the western edge of Stern Grove). Calif. Geographic Regions: **CC**: San Francisco Co. *Brandegee 1* (CAS), **SN**: Plumas Co. *Janeway 5468* (MO) and Sacramento Co. *Brandegee 25* (UC).

Riccia L. 1753
(Ricciaceae)

In number of species, this is the largest liverwort genus in California. The genus is distinguished by a) antheridia and archegonia that develop within dorsal thallus tissue, b) a sporophyte that consists of a capsule only (lacking a seta and foot), and c) a capsule that lacks sterile cells (i.e., elaters) intermixed with spores remains fully embedded in thallus tissue. Two groups or subgenera are recognized within this genus in California: (1) subgenus *Riccia*, in which the photosynthetic tissue has vertical, narrow, finger-like air-channels, and (2) subgenus *Ricciella*, in which the photosynthetic tissue has somewhat polygonal air-chambers.
Care must be taken during specimen collection and species identification, because species of *Riccia* often grow intermixed. Care also must be taken in deciding the presence or absence of cilia, because cilia development in some species appears to be facultative; i.e., normally ciliate plants may have no or only sparsely developed cilia when growing in wet or moist conditions (such as early in the rainy season). Search field populations carefully before collecting specimens for identification, and make microscope observations on several thalli.
Thirteen species in California.

Species Key

1. Photosynthetic tissue composed of large air-chambers separated by uniseriate walls, at least in young tissue near the apex; dorsal surface appearing spongy or lacunose with age in some species. . . . . **2.**

1. Photosynthetic tissue composed of uniseriate columns of cells, separated by narrow, finger-like air-channels; dorsal surface never appearing spongy or lacunose with age. . . . . **6.**
2. Plants terrestrial; sporophytes not protruding strongly on the ventral side of thallus. . . . . **3.**
2. Plants floating aquatics or terrestrial when stranded; sporophytes protruding prominently on the ventral side of the thallus. . . . . **5.**
3. Plants dioicous; female and, especially, male plants often tinged reddish; distal spore face with numerous wavy ridges that occasionally branch. . . . . **R. frostii**
3. Plants monoicous; plants seldom tinged reddish; distal spore face with complete or incomplete areolae. . . . . **4.**
4. Plants green, gray-green or yellowish-green; thallus with a spongy or lacunose appearance; spores 64–110 µm; distal spore face with 5–7 incomplete to complete areolae. . . **R. cavernosa**
4. Plants gray-green, becoming whitish when dried in the field; thallus not appearing spongy or lacunose; spores 56–84 µm; distal spore face with 7–10 complete areolae. . . **R. crystallina**
5. Thallus sparingly branched; branches usually less than 0.7 mm wide and 1.2–3 × as wide as thick. . . . . **R. canaliculata**
5. Thallus frequently branched; branches usually more than 0.8 mm wide and 3–6 × as wide as thick. . . . . **R. fluitans**
6. Thallus margin with few to many cilia. . . . . **7.**
6. Thallus margin without cilia. . . . . **10.**
7. Cilia 300–900 µm long, commonly on the dorsal thallus surface above each sporangium. . . . . **R. trichocarpa**
7. Cilia 50–400 µm long, but not present on dorsal thallus surface above each sporangium. . . . **8.**
8. Antheridial ostioles not or only little elevated above thallus surface; cilia slender and often forming an apical cluster. . . . . **R. californica**
8. Antheridial ostioles long, elevated 60–200 µm above thallus surface; cilia usually stout but not forming an apical cluster. . . . . **9.**
9. Dry mature thalli with thick apices and lateral margins usually with thick, rounded (tumid) ridges; dry thalli in cross-section 1.5–3.5 times as wide as thick. . . . . **R. beyrichiana**
9. Dry mature thalli with thin apices and lateral margins thin, not forming tumid ridges; dry thalli in cross-section 4–6 times as wide as thick. . . . . **R. glauca**
10. Ventral scales whitish to hyaline, conspicuously extending beyond the thallus lateral margin in both fresh and dry thalli. (some dry thalli of *R. sorocarpa* also can key here) **R. lamellosa**
10. Ventral scales variously colored, but not conspicuously extending beyond the thallus lateral margin in both fresh and dry thalli. . . . . **11.**
11. Ventral scales shiny black to purplish black. . . . . **R. nigrella**
11. Ventral scales hyaline to brown (but black in some populations of *R. sorocarpa*). . . . . . **12.**
12. Thallus with scattered orange oil-cells; margins of older plants brownish-orange. . . . . **R. campbelliana**
12. Thallus without orange oil-cells; margins of older plants green, hyaline, or tinged with violet, but not tinged brownish-orange. . . . . **13.**
13. Thallus broad, up to 3 mm wide; thallus of dry plants in cross-section 4–6 times as wide as thick; dry plants with thin usually flat margins; antheridial ostioles conspicuous. . . **R. glauca**
13. Thallus narrow, up to 1.8 mm wide; thallus of dry plants in cross-section 2–3 times as wide as thick; dry plants with acute margins; antheridial ostioles not conspicuous. . . **R. sorocarpa**

Riccia californica, R. campbelliana, R. lamellosa, R. nigrella, R. sorocarpa, and *R. trichocarpa* usually occur in similar hot, summer-dry locations and often in the same general area; when one is found look for the others.

Exclude. Riccia violacea M. Howe. Steere (1954) reported this species from Santa Catalina Island, Los Angeles County based on his collection of a small number of plants on exposed soil from the rocky headlands of White's Landing. No collection number was cited. A search of CAS, UC, NY, UBC and other herbaria failed to locate a Steere (or any other California) collection of this species. *Riccia violacea* could not be confirmed for California.

Riccia beyrichiana Hampe ex Lehm. (subgenus *Riccia*)

This species occurs in a range of habitats from low to high elevation and has variable vegetative morphology. Examination of spore markings from several capsules is the best way to confirm species identification.

Distinctive features. In mature thalli in drying areas, look for a) thalli with raised rounded (tumid) lateral margins (the raised margins collapse when dry), b) usually thin-walled, finely granular cilia, 75–300 μm long, at the thallus apex and on the tumid lateral margins (some cilia can be slightly on the dorsal surface because of the rounded thallus margins), c) in thallus cross-section, dry main branches 1.5–3.5 times as wide as thick, and d) older thalli often with brownish to reddish-purple lateral margins and ventral surfaces.

In thalli of wet areas (such as shaded margins of vernal pools, seepages and drainages as well as early in the growing season during winter rains or following snow-melt), look for a) thalli with flat lateral margins (not or little tumid), b) few to no cilia at the apex and lateral margins, c) in thallus cross-section, main branches 4–6 times as wide as thick, and d) older thalli light green, whitish or light yellowish-brown. For these habitats, carefully search the drier periphery or raised drier areas for more "typical" plants.

Confirm identification by details of spore markings. Sporophytes of this monoicous species mature June through October above 1000 m; May through July below 1000 m. Look for a) conspicuous hyaline antheridial ostioles 60–200 μm high, b) plants from drier habitats often with a purple coloration on the dorsal thallus tissue over capsules, c) angular pale to dark brown spores mostly 80–125 μm in diameter, d) finely granular distal and proximal spore faces and spore wing, e) mostly 5–9 areolae across the distal spore face, each areola 10–20 μm wide (occasionally some spores in a capsule will have 5–9 areolae on the distal face while other spores in the same capsule will have up to 12 areolae, each areola of correspondingly smaller diameter), and f) proximal spore face with low and/or long branched or unbranched ridges, or faint to distinct incomplete or complete areolae (in some populations, spores from the same capsule can exhibit great morphological diversity—look at more than one spore).

Separation. Riccia beyrichiana can be confused with *R. glauca*. Both species a) have rather large thalli, b) have a variable presence of marginal cilia, c) grow in slow-to-dry habitats, and d) have conspicuous, long, hyaline antheridial ostioles. Details of spore morphology are the best way to separate these two species. In *R. beyrichiana* a) all spore surfaces are finely granular (vs. spore surfaces not or only sparsely granular in *R. glauca*), b) the spores are somewhat larger, mostly 80–125 μm (vs. spores 75–100 μm), c) mostly 5–9 areolae across the distal face (vs. 8–12 areolae across the distal face), and d) the proximal spore face typically has low ridges and weakly developed incomplete and complete areolae (vs. areolae well-developed and complete).

Fresh vegetative thalli of *R. beyrichiana* growing in drying or exposed habitats can be separated from *R. glauca* by a) the thallus dorsal groove soon widening and flattening behind the apex and becoming bordered by raised, rounded (tumid) lateral ridges (vs. the thallus dorsal groove soon vanishing behind the apex and the lateral margins not bordered by tumid ridges in *R. glauca*), b) the thallus lateral margin and ventral surface often with reddish or purplish coloration (vs. thallus lateral margin and ventral surface without reddish or purplish coloration), and c) dried thalli 1.5–3.5 times as wide as thick in cross-section (vs. dried thalli 4–6 times as wide as thick in cross-section). However, vegetative thalli of *R. beyrichiana* collected early in the growing season or from wet areas (such as margins of vernal pools) often lack raised tumid ridges and reddish or purplish coloration, and the dried thalli can be 4–6 times as wide as thick in cross-section. Use details of spore morphology to identify these plants.

Illustrations. Damsholt 2002; Paton 1999; Schuster 1992b.

Habitat. On sunny to lightly shaded mineral and peaty soil; margins of vernal pools, seepages, drainages, and mountain meadows; places that are slow to dry after winter rains and snow-melt. Elevation from 140 to 3440 m; more common above 330 m.

Distribution. Riccia beyrichiana occurs in Europe, North Africa, and North America. Calif. Geographic Regions: **CC**: Monterey Co. *Doyle 7461* (UC), **CR**: Shasta Co. *Doyle 8754* (UC), **KR**: Siskiyou Co. *Norris 99782* (UC), **MP**: Modoc Co. *Doyle 6681* (UC), **SC**: Riverside Co. *Doyle 7512* (UC), **SN**: Amador Co. *Norris 82681* (UC).

Riccia californica Austin (subgenus *Riccia*)

Caution. Very young plants and plants in wet areas (early in the season or a rainy year) may have few or no cilia. At the time of collection in the field, use the hand lens to carefully search for plants with cilia, and search again under the dissection microscope in the lab.

Distinctive features. Thalli of this species typically have slender hyaline cilia on the margins and usually a conspicuous cluster at the apex; cilia, however, can be absent from older parts of the thallus.

Also look for a) light- to whitish-green thalli, usually whitish when dry and with pale yellowish brown margins in older thallus areas, b) a dorsal groove that widens close behind the apex and soon disappears, and c) usually colorless and inconspicuous ventral scales (however, some populations have plants with conspicuous black scales).

Sporophytes of this monoicous species mature late March through May. Look for a) inconspicuous antheridial ostioles, little or not elevated above the thallus surface, b) light brown spores, turning dark brown at maturity, mosly 64–89 μm in diameter, c) distal spore face with 8–13 areolae, mostly 5–9 μm wide, and with blunt papillae at areolae corners, d) proximal spore face also areolate, but not as strongly.

Separation. This distinctive species is likely to be confused only with *R. beyrichiana* and *R. glauca*. *Riccia californica* has a) inconspicuous antheridial ostioles (vs. ostioles conspicuously elevated above the thallus surface in both *R. beyrichiana* and *R. glauca*), and b) smaller spores, not exceeding 90 μm (vs. larger spores, mostly 85–125 μm).

Illustrations. Howe 1899; Schuster 1992b.

Habitat. Soil of open and lightly shaded summer-dry hillsides, meadows, grasslands, chaparral and woodlands. Elevation usually below 700 m.

Distribution. Riccia californica primarily is a California species, although Schuster (1992b) reported it from Texas. Calif. Geographic Regions: **CC**: San Luis Obispo Co. *Doyle 7230* (UC), **CR**: Tehama Co. *Doyle 5769* (UC), **GV**: Sacramento Co. *Carter 478* (UC), **NC**: Marin Co. *Doyle 8396* (UC), **SC**: Riverside Co. *Doyle 7289* (UC), **SN**: Nevada Co. *Doyle 8499* (UC).

Riccia campbelliana M. Howe (subgenus *Riccia*)

Distinctive features. Thalli of this distinctive species are 1.0–2.5 mm wide and often form large populations. The thallus has a green to gray-green dorsal groove in young and shaded plants, whereas they are distinctively bordered by a brownish-orange margin later in the season and in exposed habitats. In older, drying thalli, the entire dorsal surface is a brownish-orange or brown. Also look for a) numerous oil-cells in the dorsal epidermis, b) usually inconspicuous, pale brown to nearly hyaline ventral scales; the scales occasionally extend slightly beyond the margin, especially in dry specimens, and c) thin thallus margins that generally do not greatly incurve over the dorsal surface of dry plants.

Sporophytes of this monoicous species mature March through June. Look for a) conspicuous antheridial ostioles extending above the dorsal surface, b) yellowish-brown to brown angular spores, 83–109 μm in diameter, c) a distal spore face with numerous low, usually short sinuous ridges that seldom intersect to form areolae, and d) a proximal spore face with numerous short low ridges and papillae.

Separation. Mature plants are readily recognized in the field—the thallus has a broad gray-green dorsal groove with brownish-orange lateral margins; the entire dorsal surface can be orange-brown in plants drying in the field. Although *R. nigrella* also can have an orange-brown dorsal surface, *R. campbelliana* can be separated by a) a wider thallus, 1.0–2.5 mm wide (vs. 0.5–1.1 mm wide in *Riccia nigrella*), b) conspicuous antheridial ostioles (vs. antheridial ostioles that are not or only little exserted, and c) pale brown to nearly hyaline ventral scales (vs. shiny purplish-black ventral scales).

Illustrations. Howe 1899; Schuster 1992b.

Habitat. Exposed summer-dry mineral soil in grasslands, openings in chaparral and woodlands, sandstone outcrops, margins of ephemeral seepages on thin soil over granite rock slabs. Elevation from near sea-level to 1950 m; mostly below 1500 m.

Distribution. Riccia campbelliana has been reported from Argentina, South Africa, and Russia, as well as from the Midwest and southern states of North America. Calif. Geographic Regions: **CC**: Monterey Co. *Doyle 8072* (UC), **CR**: Tehama Co. *Doyle 5772* (UC), **GV**: Sacramento Co. *Carter 411* (UC), **NC**: Marin Co. *Carter 520* (ABSH), **SC**: Riverside Co. *Shevock 20531* (CAS), **SN**: Tulare Co. *Norris 87636* (UC).

Riccia canaliculata Hoffm. (subgenus *Ricciella*)

These aquatic or stranded plants earlier were interpreted to be the terrestrial form of *R. fluitans* because they frequently had sporophytes; contact with soil was considered to be important in inducing sexual reproduction.

Distinctive features. Look for a) sparingly branched thalli, 0.3–0.7 mm wide, with terminal branches often slightly tapered toward the apex, b) in cross-section, branches 1.2–3.0 times as wide as thick, c) small bilobed ventral scales at the branch apex, that often become divided and appear to be in two rows in older branches (the ventral scales can be nearly impossible to locate in dry specimens).

Sporophytes develop July through October. Look for a) capsules that protrude prominently from the ventral thallus surface, b) yellowish-brown spores, 79–95 μm in diameter, c) 4–6 areola across the distal face, the areolae with low walls that are slightly raised at the wall intersections, and d) markings on the proximal face less strongly developed than those on the distal face.

Separation. This species has been confused with *R. fluitans*. *Riccia canaliculata* can be separated by a) infrequently branched thalli (vs. frequently branched thalli in *R. fluitans*), b) branches mostly less than 0.7 mm wide (vs. branches mostly more than 0.8 mm wide), c) branch apices often tapered toward the apex (vs. usually round or truncate branch apices), d) in cross-section, a thallus 1.2–3.0 times as wide as high (vs. 3–8 times as wide as high), and e) plants occasionally with sporophytes (vs. sporophytes unknown in California plants and infrequently known elsewhere).

Illustrations. Damsholt 2002; Paton 1999; Schuster 1992b.

Habitat. Floating at or below the surface of ponds, lakes, reservoirs, and margins of slow-moving rivers; or terrestrial when stranded on banks. Elevation from near sea-level to 47 m.

Distribution. Riccia canaliculata occurs in Europe, Asia, North Africa, and North America. Calif. Geographic Regions: **GV**: San Joaquin Co. *Carter 240* (soil) (UC) and *Carter s.n.* (July 29, 1931, aquatic) (UC); Merced Co. *Nobs & Smith 438* (UC).

Riccia cavernosa Hoffm. (subgenus *Ricciella*)

Taxonomic misunderstanding led to plants that are now identified as *R. cavernosa*, to be determined as *R. crystallina*. Jovet-Ast (1965) recognized and resolved this taxonomic problem. As a result, herbarium specimens identified as *R. crystallina* must be re-examined. The two species are quite distinctive and easy to separate as described below.

Distinctive features. This species has a highly variable thallus color: bright green (especially in very young plants), yellowish-green, light-green, grayish-green, and occasionally tinged reddish or reddish-purple. Look for the early disintegration of the dorsal epidermis; this results in a characteristic spongy or frothy appearance even of very young thalli.

Sporophytes of this monoicous species mature late May through October. Look for a) capsules that are deeply embedded in thallus tissue and easily over-looked, except in old and dry plants, b) somewhat triangular dark brown to nearly black spores, 65–95 μm diameter, c) the distal spore face with variable markings, usually little to irregularly areolate, with long anastomosing ridges, short spurs and tubercles; however, the number and extent of completion of areolae is highly variable, even on spores from the same capsule, d) distal spore face with low and relatively thick ridges and areolae walls that are devoid of spines or other elevations at wall intersections, and e) a proximal spore face with complete and/or incomplete areolae, and ridges of variable lengths.

Separation. The characteristic spongy or frothy appearance of even extremely young plants makes it unlikely that *R. cavernosa* would be confused with any other species of *Riccia*. In contrast, the thallus of *R. crystallina* never is conspicuously spongy or frothy until dry, if then. Spore markings of the two species also are distinctive. In *R. cavernosa*, the distal spore face has low, rounded ridges and complete and incomplete areolae, and there are no protuberances or spines at wall intersections (vs. the distal spore face of *R. crystallina* always areolate with thin high walls and spines or protuberances at wall intersections).

Illustrations. Damsholt 2002; Paton 1999; Schuster 1992b; Stotler and Doyle 2004.

Habitat. Exposed, seasonally moist, usually water-retentive soils. Diverse substrates: soils of granitic, volcanic and sedimentary origin; sand, silt or mud, often admixed with organic matter; drying lake-banks; pond and stream margins; and seepages on hillsides, below cliffs, in meadows, and drainages along roads. Elevation from 15 to 3200 m; mostly below 2500 m.

Distribution. Riccia cavernosa is widely distributed in the warmer temperate areas of the Northern and Southern Hemisphere. It is widespread in North America. Calif. Geographic Regions: **CC**: Monterey Co. *Doyle 7462* (UC), **CR**: Tehama Co. *Doyle 8591* (UC), **GV**: Yolo Co. *Doyle 7502* (UC), **KR**: Siskiyou Co. *Doyle 9222* (UC), **MP**: Modoc Co. *Doyle 7483* (UC), **NC**: Glenn Co. *Howell 632*

(UC), **SC**: Los Angeles Co. *Wheeler 6345* (UC), **SN**: Tulare Co. *Shevock 17509* (CAS), **SNE**: Mono Co. *Doyle 6762* (UC)

Riccia crystallina L. emend. Raddi (subgenus *Ricciella*)

Distinctive features. The thalli lack a dorsal groove even near the apices, and usually are bluish- to grayish-green, but whitish when field-dried. Look for a) air chambers in a single layer and the underlying non-photosynthetic tissue extending nearly to the thallus margin, b) the dorsal epidermis of younger thalli remaining intact, not giving a frothy or spongy appearance, and c) older and dry thalli usually appear scruffy due to the somewhat late disintegration of the dorsal epidermis.

Sporophytes of this monoicous species mature March through July. Look for a) capsules deeply embedded in thallus tissue (and easily over-looked), b) yellow-brown to brown spores, somewhat triangular in shape, and 63–89 μm in diameter, c) regularly areolate distal spore face, mostly with 6–8 areolae across the face, the areolae 6–11 μm wide, d) the distal spore face with notched or shallowly toothed projections at corners of the areolae, e) the proximal spore face with a prominent, thin triradiate ridge and intervening facets with thin-walled areolae similar to those on the distal face, and f) an irregularly dentate or crenate wing margin.

Separation. See notes under *R. cavernosa* for separation from that species. With its bluish- to grayish-green color, flat dorsal surface lacking a groove even near the thallus apex, and spore markings, *R. crystallina* should not be confused with other species of *Riccia*.

Illustrations. Paton 1999; Schuster 1992b; Stotler and Doyle 2004.

Habitat. Partial shade to full sun; seasonally moist, summer-dry, compacted silt along trails, dirt roads and similar disturbed sites (including soil around picnic tables in coastal State Parks). Elevation from near sea-level to 350 m.

Distribution. Riccia crystallina occurs in both the Northern and Southern Hemisphere. In North America, it has been documented only from California. Calif. Geographic Regions: **CC**: Santa Cruz Co. *Doyle 9926* (UC), **NC**: Mendocino Co. *Doyle 6243* (UC).

Riccia fluitans L. (subgenus *Ricciella*)

Distinctive features. These aquatic plants float at or just below the water surface, or become stranded on soil by wind action or receding water level. With aquatic plants, look for a) thalli, mostly 0.8 mm or more wide, that frequently are branched, b) rounded to truncate branch apices, c) in cross-section, thalli 3–6 times as wide as thick, and d) semicircular ventral scales that are not bilobed or divided.

With stranded plants, look for a) thin thalli usually with a shiny dorsal surface that often appears fragile in dry plants, b) frequently branched thalli to 1.5 mm wide, and c) thallus apices rounded to truncate. In California, sporophytes have not been found in aquatic or terrestrial thalli.

Separation. This species and *R. canaliculata* both have narrow, strap-shaped thalli that occur on soil near water. See *Riccia canaliculata* for separation from that species.

Illustrations. Damsholt 2002; Paton 1999; Schuster 1992b.

Habitat. Floating at or below the surface of ponds, lakes, reservoirs, and rivers, or terrestrial when stranded on banks. Elevation from near sea-level to 1200 m.

Distribution. Riccia fluitans occurs in Europe, Asia, Africa, Australia, and North America. Calif. Geographic Regions: **DMoj**: Inyo Co. *Wolf 9766* (CAS), **GV**: San Joaquin Co. *Carter 241* (UC), **NC**: Marin Co. *Carter 534* (UC), **SN**: Plumas Co. *Nobs & Smith 1422* (UC).

Riccia frostii Austin (subgenus *Ricciella*)

Distinctive features. Thalli of this species are compact when young and also near the apices, but moderately spongiose with age and when dry. In cross-section, the thallus is a mixture of small polyhedral air-chambers and columnar air-channels. Look for a) male plants usually in small reddish rosettes (gray-green when very young), b) often reddish antheridia with conspicuous elongate ostioles, and c) dull- to grayish-green female plants, often tinged reddish in sunny habitats and on older plants.

Sporophytes mature late July through November. Look for a) angular brown spores 42–65 μm in diameter, b) a distal spore face with numerous thin, wavy ridges that seldom anastomose, and c) a similar but less strongly marked proximal spore face.

Separation. This distinctive species is not likely to be confused with other California species of *Riccia*. Look for separate grayish-green female plants and reddish male plants. Occasionally, it grows with *R. cavernosa*, which has a much more conspicuously spongiose thallus than *R. frostii*.

Illustrations. Clark and Frye 1928; Schuster 1992b.

Habitat. Silt to fine sandy deposits along river and lake margins; sites that remain damp such as bends in rivers, shaded places and banks of streams near lakes. Elevation from 44 to 2122 m.

Distribution. Riccia frostii is widely distributed in the temperate climate of Europe, Asia, and North America. Calif. Geographic Regions: **CC**: Contra Costa Co. *Norris 108167* (UC), **GV**: Sacramento Co. *Carter 379* (UC), **NC**: Marin Co. *Carter 988* (UC), **SC**: Los Angeles Co. *Wheeler 6344* (UC), **SN**: Alpine Co. *Doyle 6758* (UC), **SNE**: Mono Co. *Doyle 6761* (UC).

Riccia glauca L. (subgenus *Riccia*)

Distinctive features. Plants of this species usually lack marginal cilia, but a few short apical cilia occur in some populations. Look for a) a light green to whitish-or grayish-green thallus, 1–3 mm wide, and devoid of reddish or purplish pigmentation on the lateral margins and ventral surface, b) a narrow dorsal groove at the apex that soon vanishes in older thallus parts, c) in dry plants, very thin lateral margins, d) in cross-section, a thallus 4–6 times as wide as thick.

Sporophytes of this monoicous species mature from March through July. Look for a) prominent antheridial ostioles, elevated up to 160 μm above the dorsal surface, b) angular, brown to dark brown spores, mostly 75–100 μm in diameter, c) a distal spore face generally with 6–10 areolae, each 9–15 μm wide, the areolae tubercles at the angles, d) a proximal spore face similar to, but less strongly marked, than the distal face, and e) usually a smooth (occasionally granulose) wing surface and a crenulate wing margin that often appears (under the compound microscope) to have a somewhat thickened outer edge.

Separation. See *Riccia beyrichiana* for separation from that species.

Illustrations. Damsholt 2002; Paton 1999.

Habitat. Moist soil and shady banks. Elevation mostly below 350 m.

Geographic regions. Riccia glauca occurs in Europe, Asia, North Africa, New Zealand, and North America. Calif. Geographic Regions: **CC**: San Mateo Co. *Doyle 11437* (UC).

Riccia lamellosa Raddi (subgenus *Riccia*)

Distinctive features. Thalli of this monoicous species are light green to grayish-green, and lack reddish or purplish secondary pigmentation. Look for a) conspicuous large hyaline ventral scales that extend prominently beyond the thallus margins and form a conspicuous white border in both living and dry plants, b) relatively large thalli, 2.0–4.5 mm wide, with a sharp dorsal groove near the apex that disappears in older thallus areas.

Sporophytes of this monoicous species mature March through June. Look for a) antheridial ostioles not, or only weakly, elevated above the thallus surface, b) capsules deeply embedded in the ventral thallus tissue and easily overlooked even in dry plants, c) reddish-brown to dark brown to brownish-black spores, mostly 95–124 μm in diameter, d) an areolate distal spore face, the areolae 10–16 μm wide, e) a proximal spore face with smaller, less distinct areolae and low irregular, vermicular ridges, and f) an indistinct triradiate ridge.

Separation. Plants readily can be identified with a hand-lens because of the hyaline ventral scales that conspicuously extend beyond the thallus margins. Also definitive is the combination of grayish-green thallus, absence of secondary wall pigmentation, and small sporophytes embedded deep in the ventral thallus tissue. Occasionally, this species has been confused with *R. sorocarpa*. *Riccia lamellosa* has a) a much larger thallus, 2.0–4.5 mm wide (vs. 0.5–2.3 in *R. sorocarpa*) and b) hyaline ventral scales that conspicuously extend beyond the margins of both living, and dry thalli (vs. hyaline ventral scales that rarely extend beyond the thallus lateral margins, and which usually are visible only near the apices of dry thalli).

Illustrations. Frye and Clark 1937 (as *R. austini*); Howe 1899 (as *R. austini*); Schuster 1992b.

Habitat. Summer-dry sandy to gravelly soil; exposed to lightly shaded areas in meadows, openings in chaparral and *Quercus* woodlands. Elevation from 10 to 300 m.

Distribution. Riccia lamellosa occurs in Europe, Asia, Africa, and North and South America. Calif. Geographic Regions: **CC**: Santa Cruz Co. *Doyle 4214* (UC), **NC**: Marin Co. *Campbell s.n.* (CAS 119266), **SC**: San Diego Co. *Doyle 7198* (UC).

Riccia nigrella DC. (subgenus *Riccia*)

Distinctive features. Thalli of this species are narrow, 0.5–1.2 mm wide, with a sharp, narrow dorsal groove toward the apex, but obtuse and vanishing in older thallus areas, and glossy blackish-purple ventral scales. In young plants the dorsal surface often is a shiny gray-green. In mature and dry thalli the lateral margins are a brownish-orange. In exposed habitats, the entire dorsal surface is brownish-orange. The thallus margins usually are strongly incurved when dry, often only the glossy blackish-purple scales are exposed.

Sporophytes of this monoicous species mature March through June. Look for a) antheridial ostioles not, or only slightly, elevated above the thallus surface, b) numerous and often crowded capsules on the dorsal thallus surface, usually with a blackish spot over a mature capsule, c) dark brown to nearly black spores 67–82 μm in diameter), d) an areolate distal spore face with 7–12 areolae, each areola 5–10 μm wide, and with low, truncate tubercles at the corners of the areolae, e) an areolate proximal face with low, thick walls, and f) an often indistinct triradiate ridge.

Separation. This is a distinctive species. It can be confused with small thalli of *R. campbelliana*, which also has a brownish-orange dorsal surface and lateral margin. *Riccia nigrella* can be separated by a) thalli less than 1.2 mm wide (vs. 1.0–2.5 mm wide in *R. campbelliana*), b) glossy blackish-purple ventral scales (vs. brown to nearly colorless ventral scales), and c) areolate distal spore faces (vs. distal spore faces with low sinuous ridges that rarely form areolae).

Illustrations. Paton 1999; Schuster 1992b.

Habitat. Open summer-dry habitats; on soil of paths, hillsides, roadbanks, and cliff faces; openings in chaparral, meadows and woodlands; Elevation from 15 to 1550 m; mostly below 900 m.

Distribution. Riccia nigrella occurs in Europe, Asia, North Africa, Australia, and North America. Calif. Geographic Regions: **CC**: Monterey Co. *Doyle 6472* (UC), **CR**: Shasta Co. *Norris 72930A* (UC), **GV**: Kern Co. *Laeger 2228* (CAS), **KR**: Trinity Co. *Doyle 5823* (UC), **MP**: Modoc Co. *Doyle 4022* (UC), **NC**: Sonoma Co. *Carter 252* (UC), **SC**: San Bernardino Co. *Wagner 683* (UC), **SN**: Placer Co. *Whittemore 3523* (CAS).

Riccia sorocarpa Bisch. (subgenus *Riccia*)

Distinctive features. Thalli of this species are 0.6–1.8 mm wide. The dorsal surface is pale green, glaucous green or gray-green and usually becomes whitish with age and upon drying. Look for a) a dorsal surface with a distinct, sharp, deep, groove near the apex that becomes wider and usually disappears in older thalli, b) in thallus cross-section, branches 2–3 times as wide as high with acute lateral margins, c) terminal (epidermal) cells of chlorenchyma filaments soon collapse, leaving a thick-walled basal cup; the outer transverse wall of the sub-epidermal cells also are thick-walled, d) usually hyaline ventral scales that occasionally extend slightly beyond the thallus margin (scales can be blackish-purple on a few to many thalli in some California populations).

Sporophytes of this monoicous species mature March through September. Look for a) numerous, often crowded, sporangia, b) angular reddish to dark brown spores 60–98 μm in diameter, c) a distal spore face with both ridges and 8–12 areolae, each areola 6–11 μm wide, and with a finely granular surface texture, d) truncate papillae, 3–6 μm high at the intersection of areolae walls in the central region of the distal face, e) a proximal face with finely granular low ridges and tubercles, and f) an often indistinct triradiate ridge, with distinctly flattened facets between the ridge arms.

Separation. This species is separated from other *Riccia* species by a) its sharp, deep apical dorsal groove, which is clearly evident with a handlens, b) the acute lateral thallus margin with ascending sides, and c) reddish-brown spores, with an areolate distal face, a proximal face with short ridges, and a finely granular texture of both faces.

Illustrations. Damsholt 2002; Frye and Clark 1937; Paton 1999; Schofield 2002; Schuster 1992b.

Habitat. Soil; usually open habitats in meadows, grasslands, chaparral, oak woodlands, around rocks, base of cliffs, and along paths and roads; from 100 to 3500 m.

Distribution. *Riccia sorocarpa* occurs in Europe, Asia, Africa, New Zealand, Australia, and North and South America. Calif. Geographic Regions: **CC**: Monterey Co. *Doyle 4347* (UC), **CR**: Shasta Co. *Doyle 764* (UC), **GV**: Sacramento Co. *Carter 314* (UC), **KR**: Trinity Co. *Doyle 6634* (UC), **MP**: Modoc Co. *Doyle 7493* (UC), **NC**: Napa Co. *Carter 448* (UC), **SC**: Riverside Co. *Doyle 7432* (UC), **SN**: Inyo Co. *Shevock 15784* (CAS).

Riccia trichocarpa M. Howe (subgenus *Riccia*)

The species name *R. trichocarpa* is used in this publication, although relationship (synonymy) with *R. ciliata, R. canescens, or R. crinata* has been proposed: see Schuster (1992b), Jovet-Ast (1994), Grolle and Long (2000), Damsholt (2002), and Schumaker and Váňa (2005) for discussion.

Riccia trichocarpa is widespread in California with both the thallus and spores showing morphological variation. A combination of fieldwork, culture studies, and molecular techniques would help determine whether a single species occurs in California and the degree of affinity of *R. trichocarpa* with the species listed in the above paragraph.

Distinctive features. The most distinctive feature of the vegetative plant is the numerous long, slender, rigid, hyaline cilia on the thallus margin and usually on the dorsal surface over the sporophyte capsules. The cilia are 300–900 µm long and the walls are unequally thickened. Also look for a) light- or yellow-green dorsal surface of young thalli, which, with age, darken and the lateral margins often blacken, and b) a blackish ventral surface of mature thalli; upon drying, the black margin and ventral surface usually obscure the dorsal surface, and the hyaline marginal cilia conspicuously stand out against the black ventral surface.

Sporophytes of this monoicous species mature March through August. Look for a) antheridial ostioles elevated 50–100 µm above the dorsal surface, b) a reddish-purple spot, with or without cilia, on the dorsal surface over a sporophyte, e) brown, soon opaque, angular spores, 109–125 µm in diameter, and c) distal and proximal spore faces with broad granular walls that surround depressions.

Separation. This species is separated from all other California species of *Riccia* by a) the numerous large rigid cilia on the thallus margins and b) the distinctive spore markings.

Illustrations. Frye and Clark 1937; Howe 1899.

Habitat. Usually on bare sandy to gravelly soil that dries quickly after cessation of spring rains. Exposed and lightly shaded locations, such as meadows, hillsides, base of cliffs, creek and trail banks, and clearings in chaparral and oak woodlands. Elevation from near sea-level to 1400 m, mostly below 950 m.

Distribution. *Riccia trichocarpa* occurs in western North America. Calif. Geographic Regions: **CC**: Contra Costa Co. *Norris 100532* (UC), **MP**: Modoc Co. *Doyle 6675* (UC), **SC**: Riverside Co. *Shevock 20530* (CAS), **SN**: Fresno Co. *Doyle 6330* (UC).

Ricciocarpos Corda 1829
(Ricciaceae)

A monotypic genus.

Ricciocarpos natans (L.) Corda

Distinctive features. This is the only aquatic liverwort that normally floats like a canoe on the water surface, rather than floating at or below the surface. This plant is easily overlooked because it frequently grows intermixed with *Lemna, Spirodela, Wolffia* (aquatic flowering plants) and *Azolla* (an aquatic fern). The thallus is green to dark-green, sometimes tinged with violet, and 4–10 mm long and 4–9 mm wide. Also look for a) a persistent sharp median groove in the dorsal surface, b) conspicuous long, purplish to brownish ventral scales that hang down in the water column.

Sporophytes mature April through June. Look for a) pale-brown spores, 42–57 µm in diameter, that turn dark-brown to fuscous with age, b) an areolate distal spore face, each areola 6–8 µm wide, with conspicuous rounded spines at the angles of the areolae, and c) a similar proximal face often with an indistinct triradiate ridge.

Young terrestrial (stranded) plants are grayish- or yellowish-green with a median dorsal groove; older plants often have a reddish tint, the median dorsal groove can be absent, and the dorsal surface of dry plants often has a shiny appearance. Also look for a) small, distinct air-pores in the dorsal

epidermis and b) hyaline to violet ventral scales (that usually are difficult to locate because of the numerous rhizoids).

Separation. This distinctive aquatic species has a) thalli that float on the water surface and b) large pendent purplish ventral scales. Plants of the aquatic phase should not be confused with any other liverwort. However, terrestral plants at the drying margins of bodies of water might be confused, especially with *Riccia cavernosa*. Mature terrestrial thalli of *R. natans* have a) an intact dorsal epidermis and do not appear frothy or lacunose (vs. frothy or lacunose thalli from an early age in *R. cavernosa*), and b) small, distinct air-pores in the dorsal epidermis of mature thalli (vs. a dorsal epidermis that disintegrates and no longer exists in mature thalli).

Illustrations. Damsholt 2002; Frye and Clark 1937; Paton 1999; Schofield 2002; Schuster 1992b.

Habitat. Floating on the surface of lakes, ponds, reservoirs, ditches, and slowly moving water; or terrestrial on damp margins of drying bodies of water. Elevation from 15 to 1600 m.

Distribution. Ricciocarpos natans is nearly worldwide in distribution. Calif. Geographic Regions: **CC**: Alameda Co. *Ertter 18643* (UC), **GV**: Madera Co. *Doyle 7590* (UC), **KR**: Trinity Co. *Tracy 7787* (UC), **MP**: Modoc Co. *True & Stokes 1003* (UC), **NC**: Humboldt Co. *Abrams 7205* (CAS), **SN**: Tulare Co. *Shevock 16904* (CAS).

Targionia L. 1753
(Targioniaceae)

A distinctive feature of this genus is the development of archegonia and sporophytes at the apex of what appears to be the ventral surface of a main thallus branch. Each sporophyte is enclosed by a large, 2-valved, laterally-compressed, shiny purplish-black involucre. When dry, the thallus apex bends upwards, exposing the black scales and sporophyte. Vegetative plants have a) simple pores in the dorsal epidermis, b) air-chambers in a single thin layer with photosynthetic filaments attached to the chamber floor, c) dorsal epidermal cells with nodose trigones, d) glossy blackish ventral scales, and e) antheridia embedded in the dorsal surface of short lateral branches of ventral origin.

Two species in California.

Species Key

The following key was modified from information provided in the spring of 2005 by Alan Whittemore.

1. Midrib 0.4–0.6 the width of the thallus; cell walls in the ventral tissue (at least some walls in some cells) thickened and with elliptical pits; ventral scales subtending the involucre linear to lanceolate. . . . . **T. hypophylla**
1. Midrib 0.7 the width, or more, of the thallus; cell walls in the ventral tissue thin and rarely pitted; ventral scales subtending the involucre lingulate to semi-circular. . . . . . . **T.**, sp. nov.

Targionia hypophylla L.

Distinctive features. The thallus is green to gray-green, 1–2 cm long and 2–5 mm wide, and has both dichotomous and ventral branching. With reproductive plants, look for a) sporophytes enveloped by large, 2-valved, shiny purplish-black involucres, b) antheridia sessile, in receptacles on short lateral branches of ventral origin, c) yellow to brown to fuscous spores usually 45–85 µm in diameter, d) the distal spore face with large folds and (often incomplete) areolae that are 15–20 µm wide, and d) a finely areolate texture of both spore faces, which gives a frothy appearance to the spore. Sporophytes mature April to September.

With vegetative plants, look for a) cells of the dorsal epidermis with distinct, bulging trigones, b) purplish-black ventral surface and scales, c) a single appendage on each ventral scale, d) air-chambers containing branched and unbranched photosynthetic filaments in a single thin layer, and d) simple epidermal pores only slightly elevated above the thallus surface.

Separation. This species is easy to identify when sporophytes are present—look for large, shiny purplish-black involucres at the apices of the main branches. Vegetative plants, especially in the mountains of southern California and adjacent desert areas, however, have been mis-identified as *Asterella californica*, *Mannia californica* and *Reboulia hemisphaerica*. In these regions, thalli of *T.*

hypophylla usually have a thicker midrib, more rigid thallus and more robust growth than do thalli from coastal and more northern California habitats. Unlike *Asterella, Mannia* and *Reboulia*, however, *T. hypophylla* has air-chambers in a single thin layer.

Illustrations. Frye and Clark 1937; Paton 1999; Schofield 2002; Schuster 1992b.

Habitat. Summer-dry habitats; exposed locations and shade of chaparral, *Quercus*, and rock overhangs; shaded banks and hillsides; around and on rock outcrops; occasionally on shaded boulders with moss. Elevation from near sea-level to 1950 m.

Distribution. Targionia hypophylla occurs in Europe, Asia, Africa, Australia, and North and South America. In the United States it occurs mostly in the west coast and southwest. Calif. Geographic Regions: **CC**: Stanislaus Co. *Whittemore 6572* (CAS), **CR**: Tehama Co. *Doyle 5777* (UC), **KR**: Trinity Co. *Doyle 5860* (UC), **NC**: Colusa Co. *Kellman 2744* (CAS), **SC** San Bernardino Co. *Wagner 940* (UC), **SN**: Fresno Co. *Norris 101458* (UC).

Targionia, sp. nov.

To be described by Dr. Alan Whittemore.

Sphaerocarpoids

The Sphaerocarpoids form a small well-defined group of terrestrial and aquatic plants. Definitive features include a) the development of archegonia on the dorsal surface of the stem, each archegonium surrounded by a cylindrical, bottle-shaped involucre, b) the very short stalk or seta between the sporophyte capsule and foot never elongates, and c) elaters are absent from the capsule (instead, thin-walled, somewhat rounded cells are intermixed with the spores).

Two members of this group, *Geothallus tuberosus* and *Sphaerocarpos drewii*, are the only liverworts to be listed in the 6th edition of the Inventory of Rare and Endangered Plants of California (CNPS 2001).

In California, there are 3 genera and 7 species.

Genus Key

1. Plants aquatic, attached to the substrate; stems erect, elongate with a lateral wing-like expansion; scales in two rows on the the morphological ventral surface. . . . . **Riella**
1. Plants terrestrial; stems prostrate with lateral leaves and flask- or bottle-shaped involucres; scales absent from the ventral stem surface. . . . . **2.**
2. Plants annual, without tubers or other means of perennation; stems and leaves often nearly concealed by numerous bottle- or flask-shaped involucres; distal spore face with ridges or areolae. . . . . **Sphaerocarpos**
2. Plants perennial with tubers developing within stem tissue; stems and leaves clearly visible under involucres of reproductive plants; distal spore face smooth, devoid of ornamentation. . . . . **Geothallus**

Geothallus Campb. 1896
(Sphaerocarpaceae)

A monotypic genus.

Geothallus tuberosus Campb.

Geothallus is a rare and endangered monotypic genus endemic to the Peninsular Ranges, and coastal hills and mesas of San Diego and Riverside Counties. In San Diego Co., it has been found in small, isolated populations from the coast, east to the northwestern slope of Cowles Mountain, and south to the border with Mexico. Many of the early collection sites in San Diego Co. have been compromised by development. In Riverside Co., small populations occur in the Santa Rosa Plateau Ecological Reserve, Santa Ana Mountains. Plants should be searched for in Orange Co., as well as in northern Baja California because populations located on the slope of the Otay Mesa and ravine slope overlooking the Tijuana River are just north of the border with Mexico.

Distinctive features. Geothallus tuberosus is a dioicous plant that perennates by the development of tubers. The tubers develop within stem tissue and include the apical cell. Look for a) leaves variable in

size and shape, often with large and small lamellae, b) black tubers (in drying plants) that enable the plant to survive periods of unpredictable rainfall and drought, c) colorless rhizoids, d) absence of ventral scales, e) male and female plants of similar size, f) a dorsal stem surface not obscured by cylindrical (female plants) or flask-shaped (male plants) involucres, g) large spores, 117–145 μm in diameter separating at maturity, and h) a bald distal spore face, devoid of major markings, and proximal face with a small central areolate area. Sporophytes mature April through mid-May.

Separation. In the field, young, exposed vegetative plants of *Geothallus* can be confused with *Fossombronia* because of a similar green color and crisped appearance of leaves near the shoot apices. Look at the rhizoids with a hand-lens—*Fossombronia* has purplish rhizoids whereas those of *Geothallus* are colorless. Because of its larger size, involucres not obscuring the stem surface and large spores without distinctive markings, *Geothallus* should not be confused with any species of *Sphaerocarpos*.

Illustrations. Doyle 1962; Frye and Clark 1937; Schofield 2002.

Habitat. Gravelly soil; margins of vernal pools; flat and gently sloping areas in and near chaparral. Elevation from 25 to 550 m.

Distribution. Calif. Geographic Regions: **SC**: Riverside Co. *Doyle 9542* (capsules) (UC); San Diego Co. *Doyle 761* (capsules) (UC).

Riella Mont. 1852 (Riellaceae)

This is a genus of morphologically unusual annual, submerged aquatic plants that are attached to the substrate (or lie flat on the soil when the water level drops). Shoots consist of an erect, sparingly branched stem with an undulate, unistratose dorsal laminar wing, and rhizoids at the stem base. Two rows of lateral and two rows of small leaf-like scales occur on the stem axis. Antheridia develop serially in the wing tissue, each individually surrounded by an involucre. Archegonia develop serially on the stem, each surrounded by an involucre.

Two species in California.

Species Key

1. Archegonial involucres usually with 8 longitudinal lamellae; dioicous. . . . . **R. affinis**
1. Archegonial involucres devoid of longitudinal lamellae; monoicous. . . . . **R. americana**

The two species probably are more widespread in California than collections indicate. In addition to searching for living plants, collect dry or drying mud samples from lakes, ponds, reservoirs, and ephemeral pools. After a period of dryness, place a soil sample in a deep culture dish (or other glass container), cover with water and examine periodically with a dissection microscope.

Riella affinis M. Howe and Underw.

In California this species was first reported from Lagunita, an artificial lake on the Stanford University campus, Santa Clara Co. (Thompson 1940). In 1977 (Yeo 179 [UBC]), a second California population was discovered, having developed in a laboratory culture started from dry soil taken from the Cache Creek Settling Basin, northeast Yolo Co., Sacramento Valley.

Distinctive features. A key feature of this monoicous species is the presence of about 8 longitudinal lamellae on each archegonial involucre. Also look for a) in cross-section, a stem with a slightly flattened dorsal surface, b) lateral and ventral scales unistratose to the base, b) absence of gemmae, d) an antheridial body 120–160 μm long, e) brown spores 85–120 μm in diameter, and f) spores with the following 1) a distal face spinose, with the spines 6–15 μm long with the apices mostly truncate, slightly dilated and usually with a shallow apical depression; the spine bases mostly linked by a low network resembling areolae; and 2) a proximal spore face with truncate or obtuse spines, or tubercules, 2–5 μm long. Sporophytes mature late April through July.

Separation. This species is separated from *R. americana* by a) lamellated archegonial involucre (vs. a smooth involucre in *R. americana*), b) generally smaller spore size (85–120 μm vs. 100–130 μm), c) shorter spines on the distal spore face (6–15 μm vs. 10–24 μm), d) shorter antheridial body length (120–160 μm vs. 210–235 μm), and e) and apparent absence of gemmae (vs. gemma present in *R. americana*).

Illustrations. Howe and Underwood 1903; Schofield 2002.

Habitat. Soil; seasonally submerged margins of pools, ponds and lakes. Elevation from 14 to 65 m.

Distribution. Riella affinis occurs in Eurasia, Africa, and North America. In North America, it is known only from two California locations. Calif. Geographic Regions: **CC**: Santa Clara Co. *Thompson s.n.*, June 1940 (capsules) (YU), **GV**: Yolo Co. *Yeo 179* (capsules) (UBC).

Riella americana M. Howe & Underw.

In California, this species is known only from two collections, both from the southwest margin of Big Sage Reservoir, Modoc National Forest, Modoc Co., Modoc Plateau. The identification of the first collection (*Mason 13468a* [UC] was verified by V. Proctor [TTC]).

Distinctive features. A key feature of this dioicous species is the absence of longitudinal lamellae on the archegonial involucres. Also look for a) a somewhat elliptical stem in cross-section, b) lateral leaf scales that are mostly unistratose, but multistratose at the base, and ventral leaf scales unistratose to the base, c) multicellular gemmae on the ventral surface of young stems, d) antheridial body 210–235 μm long, e) brown to dark-brown spores 100–130 μm in diameter and f) spores with the following 1) spinose distal spore face with spines 10–24 μm long, occasionally curved, and with apices slightly dilated or acute; spine bases generally interconnected by a basal membrane, but seldom form well-defined areolae; and 2) proximal spore face with spinose or with short tubercules, the spines 3–6 μm long. Sporophytes mature August through September.

Separation. See discussion under *R. affinis*.

Illustrations. Frye and Clark 1937; Howe and Underwood 1903.

Habitat. Soil; seasonally submerged in margin of a reservoir. Elevation about 1615 m.

Distribution. Riella americana is a New World species; it has been reported from North America, Mexico, and South America. In North America it has been reported in greatly disjunct populations in California, Texas, New Mexico, and South Dakota. Calif. Geographic Region: **MP**: Modoc Co. *Mason 13468a* (young capsules) (UC); *Laeger 3100* (vegetative) (CAS).

Sphaerocarpos Boehm. 1760
(Sphaerocarpaceae)

Sphaerocarpos is a genus of dioicous, short-lived annual plants. The gametophyte consists of a relatively broad, thin stem with succubous, mostly unistratose lateral leaves. There are no underleaves or scales, and the rhizoids are colorless. Antheridia and archegonia are individually enveloped by cylindrical (female) or flask-shaped (male) involucres. In most species, male plants are noticeably smaller than female plants. The antheridial and archegonial involucres usually obscure the dorsal stem surface. The antheridial involucres usually develop a reddish-purple coloration, especially in sunny habitats. Female plants and involucres usually are a light green, but develop reddish areas on involucres in sunny exposures. Involucres on female plant are cylindrical when fertilization does not occur, and nearly globose at the base when containing sporophytes. Sporophytes consist of a capsule, a very short seta and a foot. Elaters are lacking, but thin-walled cells (that are filled with starch grains during early spore development) are intermixed with spores. **Note: spore markings are distinctively species-specific.**

Four species in California.

Gametophytes of all four species collected in the field exhibit such great environmentally induced morphological variation that species identification of plants without spores can be difficult at times. Observations on spore markings, which can be discerned even on very young developing spores, are the most accurate way to identify field-collected plants. Another reason to examine immature capsules is that spores of some species are nearly opaque when mature and spore markings then can be difficult to discern. February to June is the best time to collect plants that have developing to mature spores.

Species Key

1. Spores separating long before capsule maturity. . . . . **S. cristatus**
1. Spores remaining united in tetrads after capsule dehiscence. . . . . **2.**

2. Spores lamellate with low, thick, nearly parallel ridges (a few areolae occasionally occur in the middle of the outer face of each spore). . . . . **S. drewiae**
2. Spores areolate, never with parallel ridges. . . . . **3.**
3. Areolae with prominent protuberances at the corners of the areolae (view in silhouette). . . . . **S. michelii**
3. Areolae of spores lacking prominent protuberances at the corners of the areolae (view in silhouette). . . . . **S. texanus**

Caution. It is often difficult to distinguish between field-collected plants of *S. drewiae, S. michelii*, and *S. texanus*. The female plants are larger than the male plants and usually are more easily located. Male plants are very small, reddish, and often nested within clusters of female plants. The sizes and shapes of the female plants, including sizes and shapes of the involucres, vary with the microhabitat (e.g., moisture availability, exposure).

Sphaerocarpos cristatus M. Howe

Distinctive features. This species often occurs in large patches. Search populations for female plants with capsules and the slightly smaller male plants (often with reddish coloration). In plants with capsules, look for a) yellow- to light-brown spores, 62–78 µm in diameter, that separate long before capsule maturity, b) spores with somewhat sinuous spore markings, often of nearly parallel ridges (cristae) that occasionally branch and anastomose to form a few areolae, and c) ridges on spores that often extend from one pole to the other. Rarely, are spores completely areolate (an exception: *Doyle 8457* [UC], El Dorado Co., Sierra Nevada western foothills, where both completely areolate and typical cristate spores occur in the same capsule; both cristate and areolate spores separate long before capsule maturity as is typical for *S. cristatus*).

Sporophytes mature late March through June.

Separation. Sphaerocarpos cristatus readily can be identified because the spores separate long before maturity (vs. spores remaining united in tetrads in the other three species of *Sphaerocarpos*).

Illustrations. No accurate illustrations are yet published of mature female and male plants, unfortunately, the illustrations in Howe 1899 and Frye and Clark 1937 are inaccurate renderings of very young plants.

Habitat. Plants occur in small patches or as extensive mats in slow-to-dry habitats; silty to gravelly soil of flat areas and hillsides, near and under chaparral and oaks, gardens, dirt roads, paths, banks of rivers, and margins of drainages; occasionally on rocks in splash of ephemeral creeks. Elevation from 7 to 900 m, but more common between 30 and 725 m.

Distribution. Sphaerocarpos cristatus is endemic to Californa. Although not rare, its distribution is imperfectly documented. Calif. Geographic Regions: **CC**: Contra Costa Co *Shevock 15033* (CAS), **GV**: Kern Co. *Laeger 1215* (CAS), **NC**: Mendocino *Doyle 6206* (UC), **SC**: Ventura Co. *Sagar 002* (SFV), **SN**; Fresno *Mueller 1215* (UC).

Sphaerocarpos drewiae Wigglesworth

This is a rare and endangered species endemic to the Peninsular Ranges and coastal hills and mesas of southern California. In Riverside Co., small populations occur in the San Jacinto, Santa Margarita and Santa Rosa Mts. In San Diego Co, small populations occur on the Kearney and Otay Mesas, Soledad Mt., and the hills and mesas between the coast and the Laguna Mts.

Distinctive features. Spores of this species remain united in tetrads at maturity; tetrads are 125–163 µm in diameter. When possible, make observations on spores from immature capsules because mature spore tetrads are dark-brown to black and opaque at maturity. If only mature spores are available, use reflected light and the highest magnification of the dissection microscope. Look for dark, thick, more-or-less parallel ridges that occasionally branch and anastomose, and form one or more areolae at the center of the distal spore face. Sporophytes mature late January through May (depending upon the time of onset of the rainy season).

Separation. The dark, thick, somewhat parallel ridges on spore tetrads easily separate *S. drewiae* from both *S. michelii* and *S. texanus*, which have areolate spore tetrads. These features can be observed on developing spore tetrads soon after meiosis.

Illustrations. Wigglesworth 1929; Frye and Clark 1937.

Habitat. Exposed and easily disturbed gravelly soil under and near chaparral, near vernal pools, margins of drainages, along dirt paths, and on road-cuts. Elevation between 25 and 1450 m, but usually from 100 and 650 m.

Distribution. Sphaerocarpos drewiae is endemic to southern California. Calif. Geographic Regions: **SC**: Riverside Co. *Doyle 2426* (UC); San Diego Co. *Doyle 6171* (UC).

Sphaerocarpos michelii Bellardi

Distinctive features. Spore tetrads are 85–120 µm in diameter, brown to dark-brown, and often opaque at maturity. Look for a) areolate spores, which appear somewhat spinose in profile because of prominent protuberances at the intersections of areolae walls, and b) 6–10 areolae across the distal spore face, with the the areolae 8–17 µm wide. **Note:** Occasionally, there is a single papilla in the center of an areola. Stieperaere, Arts and De Bock (1988) suggested that the presence of such a papilla in each areola of a spore is a species-determining characteristic. On the other hand, Thompson (1948) previously had reported that a papilla may or may not be present even on spores from the same capsule. Observations on California populations by the senior author agree with those of Thompson's and it is concluded that the prominent protuberances at wall intersections, not the presence of papillae, is important in identification of North American populations of this species. Sporophytes mature late May through early August.

Separation. Spores of this species superficially can be confused with those of *S. texanus*. In *S. michelii* a) areolae have an elevated protuberance at the angles between adjacent areolae (vs. the absence of such protuberances in *S. texanus*, b) spore tetrads are smaller (85–120 µm vs. 125–171 µm), and c) generally, there are more areolae across the spore face (6–10 vs. 4–6 in *S. texanus*). **Caution:** Be careful with measurements because some populations of both *S. michelii* and *S. texanus* have tetrads with two larger spores and two smaller ones; the number and width of areolae can be variable even on spores of the same tetrad.

Illustrations. Paton 1999; Schuster 1992a; Thompson 1948.

Habitat. Summer-dry soil of hillsides, and banks and floodplains of creeks; usually in the partial shade of *Pinus* and other conifers. Elevation usually from 1400 to 1900 m.

Distribution. Sphaerocarpos michelii occurs in Europe, and North and South America. Calif. Geographic Regions: **MP**: Lassen Co. *Doyle 828* (UC); Modoc Co. *Doyle 7489* (UC).

Sphaerocarpos texanus Austin

This is the most common species of the genus in California and the one most likely to be collected.

Distinctive features. Spore tetrads are mostly 125–171 µm in diameter, light- to dark-brown, and often opaque when fully mature. Look for a) areolate spore tetrads that are not spinose in profile (lacking prominent protuberances at areolae wall intersections) and b) 4–6 areolae across the distal spore face, the areolae 13–26 µm wide. Sporophytes mature mid-March through June.

Separation. Because this species often grows intermixed with, or in close proximity to, the other three species, collection of plants with developing spores is very important. See *S. michelii* for separation from that species, and *S. drewiae* for separation from that species.

Illustrations. Howe 1899; Paton 1999; Schofield 2002; Schuster 1992a; Thompson 1948.

Habitat. Often a weedy pioneer on easily disturbed summer-dry sites; on soil of hillsides, dirt roads, trails, creek banks, meadows, and margins of ephemeral seepages; open areas in chaparral and woodlands. Elevation from 10 to 1940 m.

Distribution. Sphaerocarpos texanus is widely distributed worldwide: Europe, North Africa, Australia, and North and South America. Calif. Geographic Regions: **CC**: Alameda Co. *Norris 87182* (UC), **CR**: Butte Co. *Griggs 1037* (CHSC), **GV**: Sacramento Co. *Howell 360* (CAS), **KR**: Trinity Co. *Doyle 5846* (UC), **NC**: Sonoma Co. *Eastwood s.n.* (CAS 119198), **SC**: San Diego *Doyle 7151* (UC), **SN**: Kern Co. *Shevock 14850* (CAS).

Simple Thalloid Liverworts

The simple thalloid liverworts form a morphologically diverse group of mostly thalloid plants, but it includes a few leafy liverworts as well (e.g., *Fossombronia*). Features that characterize this group are: a) development of archegonia and antheridia on the dorsal surface of a main stem or lateral branch, b) lack of underleaves, and c) presence of only smooth-walled rhizoids.

Simple thalloid liverworts differ from complex thalloid liverworts by a) the lack of pores in the dorsal epidermis and air-spaces in the underlying photosynthetic tissue (vs. generally with epidermal pores and with internal air-spaces present in complex thalloid liverworts) and b) only smooth-walled rhizoids (vs. both smooth-walled and pegged rhizoids). Simple thalloid liverworts are separated from hornworts by the presence of many chloroplasts in all thallus cells (vs. hornworts have only a single chloroplast in each cell of the thallus apex [some California hornworts have 2 chloroplasts in some mature cells]). *Fossombronia*, the only California leafy member of this group, is separated from the leafy liverworts by the continued apical growth of the stem during formation of archegonia, resulting in archegonia and sporophytes sequentially developed on the dorsal stem surface (vs. archegonia development terminating the apical growth of the branch, resulting in archegonia and sporophytes terminal at the apices of a main stem or short lateral branch in leafy liverworts).

In California, there are 7 genera, 13 species, and 2 previously reported species excluded from the flora.

Genus Key

1. Plants clearly differentiated into stem and leaves; rhizoids purple. . . . . **Fossombronia**
1. Plants thalloid with entire or somewhat lobed margins; rhizoids colorless or brownish. . . **2.**
2. Thallus margin lobed; cyanobacteria colonies on the ventral side of the thallus; gemmae multicellular, stellate and usually present at the thallus apex; long-necked flask-shaped gemma-receptacles occasionally on the dorsal surface. . . . . **Blasia**
2. Thallus margin plane or crisped, but not lobed; cyanobacteria colonies absent; gemma-receptacles absent. . . . . **3.**
3. Thallus with a conspicuous, narrow stem-like midrib and clearly unistratose wings. . . . . . **4.**
3. Thallus with an indistinct midrib, gradually thinning to the wing margins. . . . . **5.**
4. Thallus with few to many unicellular cilia on the wing margin and ventral midrib surface; midrib without a central strand of elongate, thick-walled cells; antheridia and archegonia developing on dwarf branches of ventral origin. . . . . **Metzgeria**
4. Thallus lacking unicellular cilia on wing margin and ventral midrib surface; midrib with a central strand of elongate, thick-walled cells; antheridia and archegonia developing on the dorsal surface of a main thallus or branch. . . . . **Pallavicinia**
5. Thallus usually less than 2 mm wide; cells with 0–5 large, usually brownish, oil-bodies. . . . . **Riccardia**
5. Thallus 2–9 mm wide; cells with 6 to more than 30 small, colorless oil-bodies. . . . . **6.**
6. Antheridia and archegonia developing on short lateral branches; 1-celled slime-hairs on the ventral surface at the thallus apex. . . . . **Aneura**
6. Antheridia and archegonia developing on the dorsal surface of a main axis; 2–6 celled slime-hairs on the ventral surface at the thallus apex. . . . . **Pellia**

Aneura Dumort. 1822
(Aneuraceae)

These dioicous plants are sparingly and irregularly branched. The thallus is rather fleshy and has an indistinct midrib. There are 6 to many small oil-bodies per thallus cell. Archegonia and antheridia develop on short lateral branches.

One species in California.

Aneura pinguis (L.) Dumort.

Distinctive features. Plants of this species are sparingly and irregularly branched. The branches of living plants usually are opaque and brittle, and generally have a greasy luster. Thallus color usually is light- to dark-green, but somewhat bluish plants have been found in the high Sierra Nevada (e.g., *Laeger 1977* [CAS]); the bluish color fades to green upon drying. Also look for a) the center of the thallus 7–18 cells thick in thallus cross-section, and gradually thins toward the margin, b) 6 or more small oil-bodies in each cell, c) male plants usually smaller than female plants, d) antheridia embedded

in short lateral branches, and e) archegonia developing on lateral branches that are mostly hidden by the reflexed margin of the branch.

Separation. Vegetative plants of *Aneura pinguis* can be confused with the liverworts *Pellia* and *Riccardia* and the hornwort *Phaeoceros*. In contrast to *Riccardia*, *Aneura* has a) an indistinct midrib region (vs. a more distinct midrib in *Pellia*, and b) an opaque, brittle and greasy appearing thallus (vs. a somewhat translucent, non-brittle and non-greasy appearing thallus). Small thalli of *Aneura* can be confused with *Riccardia*. However, *Aneura* has a) 6 or more small oil-bodies per cell (vs. 0–3 large oil-bodies per cell in *Riccardia*) and b) a thallus that is greasy in appearance (vs. a non-greasy appearing thallus). *Aneura* is separated from *Phaeoceros* by a) cells near the thallus apex each with several chloroplasts (vs. cells near the thallus apex each with one chloroplast in *Phaeoceros*) and b) absence of colonies of cyanobacteria in the ventral thallus tissue (vs. presence of colonies of cyanobacteria in the ventral thallus tissue).

Illustrations. Damshot 2002; Frye and Clark 1937; Paton 1999; Schofield 2002; Schuster 1992a.

Habitat. Wet shaded soil, rocks, and organic matter of stream banks, ditches, marshes, and seepages. Elevation from about 12 to 3620 m.

Distribution. Aneura pinguis is widely distributed in the Northern and Southern Hemispheres. Calif. Geographic Regions: **CC**: Contra Costa Co. *Mason 2486* (UC), **CR**: Shasta Co. *Doyle 9863* (UC), **DMoj**: Inyo Co. *Laeger 1229* (CAS), **KR**: Siskiyou Co. *Shevock 20078* (CAS), **MP**: Modoc Co. *Doyle 8645* (UC), **NC**: Humboldt Co. *Bourell 3677* (CAS), **SC**: San Bernardino Co. *C. Wagner 815* (UC), **SN**: Tuolumne Co. *Laeger 1977* (CAS).

Blasia L. 1753
(Blasiaceae)

Blasia is a distinctive thalloid genus separated from other California liverworts by a) a thallus with clearly lobed lateral margins, b) multicellular, stellate gemmae at the thallus apex, c) long-necked, flask-shaped gemma-receptacles on the dorsal thallus surface, and d) the usual presence of colonies of cyanobacteria in small scale-like auricles at lobe bases on the ventral thallus surface.

Note. This genus traditionally has been classified with the simple thalloid liverworts. However, He-Nygrén, et al. (2006) recently have shown that *Blasia* should be classified with the complex thalloid liverworts. Two morphological characters that it shares are the development of two rows of ventral scales and the presence of gemma-receptacles. In this publication, *Blasia* is included in the simple thalloid liverworts for the convenience of keying plants.
A monotypic genus.

Blasia pusilla L.

Distinctive features. The thallus of this dioicous species is light- to dark-green. Look for a) a thallus with an ill-defined midrib that grades gradually into unistratose wings with scalloped, often leaf-like lobes, b) two kinds of multicellular gemmae: 1) flat, stellate, multicellular gemmae usually present at the thallus apex and 2) slightly flattened, circular gemmae that develop in long-necked, flask-shaped gemma-receptacles on the dorsal thallus surface, c) two rows of scales on the ventral surface of the midrib, and d) two rows of cyanobacteria colonies that occur in scale-like auricles at the base of the lobes on the ventral thallus surface.

Separation. This is a very distinctive thalloid liverwort. Diagnostic in the field, and visible with the hand-lens, are a) the lobing of the thallus margin, b) stellate gemmae usually present at the thallus apex, and c) cyanobacteria colonies present on the ventral thallus surface. On casual observation, plants of *B. pusilla* without gemmae can be confused with gametophytes of hornworts and the liverworts *Aneura pinguis* and *Pellia* species. Hornworts, however, a) lack scales on the ventral thallus surface, b) have cyanobacteria colonies within (endogenous) thallus tissue, c) have a single, large chloroplast in cells at the thallus apex, and d) lack gemmae. Unlike *Blasia*, *Aneura pinguis* and *Pellia* spp. lack a) scales on the ventral thallus surface, b) association with cyanobacteria colonies, and c) stellate gemmae or gemmae in specialized structures.

Illustrations. Damsholt 2002; Paton 1999; Schofield 2002; Schuster 1992a; Smith 1990.

Habitat. Wet, shaded gravelly and clayey soil of stream floodplains, banks of creeks and ditches, and margins of marshy areas. Elevation from 25 to 830 m.

Distribution. *Blasia pusilla* occurs in cooler areas of Europe, Asia, and North America. Calif. Geographic Regions: **KR**: Del Norte Co. *Doyle 2007* (UC), **NC**: Humboldt Co. *Doyle 10962* (UC). (The report of *B. pusilla* in Santa Barbara Co. was based on a mis-identification. The 1921 C. C. Haynes collection (CAS, NY) from the Hope Ranch, Santa Barbara Co. identified as *B. pusilla* contains vegetative plants of *Phaeoceros* cf. *pearsonii*).

Fossombronia Raddi 1818
(Fossombroniaceae)

This is the only California genus of simple thalloid liverworts in which the shoot is differentiated into stem and leaves. *Fossombronia* is readily recognized with a 10× handlens. Look for a) stems with succubous leaves and long purplish rhizoids, b) archegonia and whitish or yellowish-orange antheridia naked on the dorsal stem surface of main branches, c) a conspicuous cup-like pseudoperianth around each sporophyte, and d) stem growth and sex organ development continuing after fertilization so that more than one sporophyte often occurs on the same branch. All California plants can develop tuberous stem apices at the end of the growing season. These modified stem tips permit survival of conditions when water is unavailable for growth (drought in lower elevation, summer-dry habitats and freezing in higher elevation, winter-snow habitats). When favorable growing conditions re-occur, plants can resume growth from these apices.

In general, the vegetative morphology of plants of lower elevations (below 1400 m), and especially plants of the North, Central, and South Coast Regions, often exhibit variability in color, leaf shape, and manner of leaf insertion on the dorsal stem surface. At least some of this variation appears to be related to seasonal changes during the growing season (e.g., rainfall, cloud cover, onset of dormancy), substrate (e.g., rapidity or slowness of substrate drying between rain events), and exposure. This morphological variability makes it difficult to use vegetative characters alone to identify plants.

On the other hand, details of spore morphology have proven useful to separate California species. The spore characters used in the following key are consistent within a capsule and in several capsules occurring on the same branch of a single plant. Because antheridia and archegonia continuously develop throughout the growing season on reproductively mature plants, a new crop of capsules with mature spores usually develops about 2 weeks following a rain event.

Two species in California.

Species Key

1. Spores typically with 11 to 28 lamellae around the circumference as seen in equatorial optical section with the compound microscope; lamellae of spores spaced 4.5–10 µm apart, in side view; leaf attachment usually does not exceed the midline on the dorsal stem surface of vegetative plants. . . . . **F. pusilla**
1. Spores typically with 30 to 44 lamellae or spines around the circumference as seen in equatorial optical section with the compound microscope; lamellae or spines of spores spaced 1.5–3.5 µm apart, in side view; leaf attachment usually exceeds the midline on the dorsal stem surface of vegetative plants. . . . . **F. longiseta**

Fossombronia longiseta (Austin) Austin

The treatment of this species by Howe (1899) is a composite of the two species recognized here.

Distinctive features. Vegetative plants can exhibit great morphological variation on the same shoot during a single growing season, depending upon temporal variation in moisture, sunlight and maturity level. Search for capsules at the apices of nearly fully elongated setae. Spores in capsules before seta elongation (related to water stress or premature death by collection) often have shorter lamellae and spine heights than do spores in capsules in which the seta has elongated. Look for a) spores with 30 or more lamellae or spines as seen in equatorial optical section with the compound microscope, b) in side view, spores with closely spaced lamellae or spines, 1.5–3.5 µm apart, c) mature spores 40–53 µm in diameter, and d) elaters from 125–290 µm long and with 2 (occasionally 3 in the elater middle) thickened helical bands. There is variation in spore markings, often within the same capsule. At one extreme are spores that are entirely echinate; at the other extreme are spores only with lamellae. The lamellae can a) extend unbranched from one side across the distal face to the other side, b) divide and anastomose to form one to several areolae on the distal face, c) be a mixture of short and long

lamellae; d) be a mixture of mostly short lamellae on the side and entirely echinate on the distal face, and e) be a mixture of short lamellae and spines on both the side and distal face, etc. When we rely soley on spore markings to delimit the two California species, none of the variations consistently correlate with the variations in vegetative morphology.

Vegetative plant color and morphology, including leaf size and shape, are variable within and among populations and it often is not possible to be sure of species identification without examination of spore markings. In general, the attachment of the leaf base extends across the midline on the dorsal stem surface, but this not always true. In addition, pseudoperianths usually lack lamellar outgrowths on their outer surface, but lamellar outgrowths do occur on some pseudoperianths of populations with *longiseta*-type spores.

Separation. In general, *F. longiseta* frequently occurs in more exposed, quicker to dry sites than does *F. pusilla*. As indicated in the key, however, the number of lamellae as seen in equatorial optical section with the compound microscope is the simplest and quickest way to separate these two species. In field-collected material, both *F. longiseta* and *F. pusilla* exhibit similar diversity in vegetative plant morphology, including leaf size and shape, place of leaf attachment on the dorsal stem surface (up to or beyond the stem middle), and development of tuberous stem apices. Use non-spore features with caution in separation of these two species. Recognizing that there are exceptions, *F. longiseta* generally has a) leaf base attachment that extends across the midline on the dorsal stem surface (vs. leaf base attachment that does not extend across the midline in *F. pusilla*) and b) pseudoperianth often without lamellar outgrowths (vs. pseudoperianth usually [not always] with lamellar outgrowths).

Illustrations. Howe 1899 (Figs. 17, 19 and 20 only); The treatment of *Fossombronia longiseta* in Schuster (1992a) is based on specimens that do not belong to that species.

Habitat. Generally exposed clay, silty and gravelly soil of hillsides, road banks, paths, and base of sandstone and other rock outcrops. Elevation from 140 to 1415 m.

Distribution. Fossombronia longiseta occurs in western North and South America. Calif. Geographic Regions: **CC**: Monterey Co. *Doyle 11352* (UC), **NC**: Glenn Co. *Doyle 6303* (UC), **SC**: Santa Barbara Co. *Doyle 10349* (UC), **SN**: Fresno Co. *Shevock 17128* (CAS).

Fossombronia pusilla (L.) Nees

This is the first published report to confirm the occurrence of *Fossombronia pusilla* in North America. As Schuster (1992b) pointed out, earlier reports of *F. pusilla* from eastern North America are suspect at best. Morphologically, the California populations of this species are indistinguishable from those of Europe (see Stotler and Crandall-Stotler 2005b).

Distinctive features. As in *F. longiseta*, vegetative plants can exhibit color and morphological variation. Spore markings are the most straight-forward way to identify this species. Look for a) with the compound microscope, spores with 16–28 lamellae in equatorial optical section, b) in side view, spores with lamellae 4.5–10 µm apart, c) mature spores 38–55 µm in diameter, and d) elaters 130–250 µm long and with 2 (occasionally 3 in the elater middle) thickened helical bands. In vegetative plants, the leaf base on the dorsal stem surface generally does not cross the stem midline. In addition, pseudoperianths often (not always) have short or long lamellar outgrowths on their outer surface.

Separation. See *F. longiseta* for separation from that species.

Illustrations. Damsholt 2002; Howe 1899 (Figs. 16 and 18); Paton 1999; Smith 1990.

Habitat. Damp shaded places somewhat slow-to-dry after spring rains or snow-melt; soil and organic matter of meadows, lake and stream banks, rock outcrops. Elevation from 9 to 2670 m.

Distribution. Fossombronia pusilla occurs in Europe, Asia, Africa, Australia, and North America. Calif. Geographic Regions: **CC**: San Mateo Co. *Doyle 10386* (UC), **CR**: Shasta Co. *Doyle 9344* (UC), **KR**: Siskiyou Co. *Doyle 9158* (UC), **MP**: Modoc Co. *Doyle 7495* (UC), **NC**: Lake Co. *Doyle 8362* (UC), **SC**: San Diego Co. *Doyle 9535* (UC), **SN**: Mariposa Co. *Shevock 21451* (CAS).

Metzgeria Raddi 1818
(Metzgeriaceae)

Thalli of this genus are long and strap-shaped, usually less than 2 mm wide, and have a) a narrow, sharply defined midrib (costa) that lacks elongate, thick-walled cells, b) unistratose wings, and

c) dwarf sexual reproductive branches developing from the ventral surface of the midrib. California species have a variable development of unicellular cilia (hairs) on both the wing margin and midrib ventral surface.

Two species confirmed in California. See Grolle and So (2003) for use of the species name *Metzgeria violacea* rather than *M. fruticulosa.*

Species Key

1. Midrib usually with 2–3 rows of cells on the dorsal surface and mostly 3–5 rows of cells on the ventral surface; marginal cilia of the wing mostly in pairs (some are single); gemmae absent. . . . . **M. conjugata**
1. Midrib usually with 2 rows of cells on the dorsal surface and mostly 2–3 rows of cells on the ventral surface; marginal cilia of the wing usually single; gemmae developing on specialized attenuated branches. . . . . **M. violacea**

Excluded. Metzgeria temperata Kuwah. Kuwahara (1976) segregated this species from *M. fructiculosa* (Dicks.) A. Evans. Based on *Yurky 166*, Yurky (1995) reported *M. temperata* from Marin County. Damsholt (2002) and Paton (1999) provided detailed descriptions and excellent illustrations of both *M. temperata* and *M. fruticulosa* (=*M. violacea*). Examination during this study found that *Yurky 166* had the definitive characteristics of *M. violacea. M. temperata* could not be confirmed for California.

Metzgeria conjugata Lindb.

Distinctive features. This monoicous species usually occurs in loose green or pale-green mats. Look for a) marginal thallus wings recurved, b) a midrib 2–3 cells wide as seen from the dorsal surface and 3–5 cells wide on the ventral surface as seen from the ventral surface, c) cilia commonly present on wing margins and ventral midrib surface, d) marginal cilia straight or slightly curved, in pairs or single, and e) attenuated branches with gemmae absent.

Separation. This species is separated from *M. violacea* by a) marginal cilia usually in pairs (vs. marginal cilia mostly single in *M. violacea*), b) the dorsal midrib surface mostly 2–3 cells wide and the ventral surface 3–5 cells wide (vs. the dorsal midrib surface 2 cells wide and the ventral surface mostly 2–3 cells wide), and c) the absence of gemmae development (vs. the frequent development of gemmae in *M. violacea*).

Illustrations. Damshot 2002; Paton 1999; Schofield 2002; Schuster 1992a; Smith 1990.

Habitat. In diffusely lit, humid areas; on bark of shrubs and angiosperm trees, and rock outcrops. Elevation from 30 to 250 m.

Distribution. Metzgeria conjugata occurs in Europe, Asia, Africa, and North and South America. Calif. Geographic Regions: **KR**: Del Norte Co. *Doyle 1995* (UC), **NC**: Humboldt Co. *Doyle 2114* (UC).

Metzgeria violacea (Ach.) Dumort.

Although many collections of this species develop a persistent postmortem bluish coloration of the whole shoot, California specimens mostly develop a bluish coloration only in the shoot apices and erect, attenuated gemmiferous branches. The bluish coloration often takes months for maximum development and it persists for years. However, do not use the presence or distribution of color as the only guide to species identification.

Distinctive features. Look for a) relatively short branches, generally less than 1.5 cm long, b) widest region of the wing mostly 9–12 cells wide, c) cells in the middle of mature wing tissue that are mostly 17–30 μm wide × 22–45 μm long, d) dorsal midrib surface with 2 rows of cells, and ventral surface with 2–4 rows of cells, e) attenuated gemmiferous branches usually erect, with gemmae on both wing margins and midrib tissue, and usually with an apical cluster of gemmae, f) central cells of the dorsal gemma surface without protruding conical walls, and g) adventitious shoots common (with the midrib cells of the adventitious shoot occasionally not connected to the midrib of the main branch).

Separation. See *Metzgeria conjugata* for separation from that species. *M. violacea* can be confused with *M. temperata*. It can be separated by a) shorter shoots, 0.4–1.5 cm long (vs. shoots mostly 1.5–

2.5 cm long in *M. temperata*), b) smaller wing cell size, 17–30 μm wide × 22–45 μm long (vs. wing cell size 25–43 μm wide × 33–58 μm long), c) ventral midrib surface with 2–4 rows of cells (vs. ventral midrib surface with 2 (occasionally 3) rows of cells), d) adventitious shoots common (vs. adventitious shoots uncommon), e) gemmae from midrib and wing margins (vs. gemmae only from wing margins), and f) central cells of the the dorsal gemma surface without conical protuberances (vs. central cells of the dorsal gemma surface with conical protuberances).

Illustrations. Damsholt 2002 (as *M. fruticulosa*); Paton 1999 (as *M. fruticulosa*).

Habitat. Trunks of shrubs in shaded, humid understory of redwoods, and mixed hardwood/conifer forest. Elevation under 430 m.

Distribution. Metzgeria violacea occurs in Europe, Asia, and North America. Calif. Geographic Regions: **NC**: Humboldt Co. *Kofranek 1589* (UC) and Marin Co. *Yurky 166* (a robust, gemmiferous population) (SFSU).

Pallavicinia Gray 1821
(Pallaviciniaceae)

Distinctive features of this genus include a) a narrow and distinct midrib with a well-defined central strand of elongate, thick-walled cells, b) a unistratose wing, c) absence of cilia on the wing margin and midrib, d) antheridia in two rows, one row on each side of the midrib dorsal surface, and e) archegonia in groups on the dorsal surface of the midrib. This genus should not be confused with any other.

One species in California.

Pallavicinia lyellii (Hook.) Carruth.

Distinctive features. Thalli of this dioicous species are pale to deep-green and usually translucent. Look for a) sparingly branched thalli with a distinct midrib and unistratose wings, b) a well-defined central strand of elongate, narrow diameter, thick-walled cells in the midrib (usually visible with transmitted light of the dissection miscoscope), c) absence of cilia on both the midrib and wing, d) over 30 oil-bodies per thallus cell, e) male plants with antheridia, each subtended by a scale, in two rows, one row on each side of the midrib dorsal surface, and f) female plants with archegonia in groups on the dorsal surface of the midrib and surrounded by basally fused scales or lamellae.

Separation. The presence in the midrib of a clearly defined central strand of elongate, thick-walled cells separates *P. lyellii* from all other California liverworts.

Illustrations. Damsholt 2002; Paton 1999; Schuster 1992a; Smith 1990.

Habitat. In California, in a moist recess in a rotten log, and on soil (D. Wagner, personal communication). Elevation about 91 m.

Distribution. Pallavicinia lyellii occurs in Europe, Asia, Africa, and North, Central, and South America. It mostly occurs in the eastern and central states of North America. In the west, it is known only from a single collection in California—from a second growth redwood forest on the campus of Humboldt State University, Arcata. Calif. Geographic Regions: **NC**: Humboldt Co. *Wilson 1534* (NY, CAS).

Pellia Raddi 1818
(Pelliaceae)

Species of this genus have a) a definite, but rather poorly delimited midrib that gradually thins toward the margin, b) often undulating wings, c) no central strand of elongate, thick-walled cells in the midrib, d) 2–8-celled slime-filaments near the apex of the thallus ventral surface, e) rhizoids that are brownish rather than hyaline, f) antheridia individually embedded in chambers in the midrib of the dorsal thallus surface, and g) small groups of archegonia that develop in a depression on the thallus dorsal surface.

Two species in California.

Species Key

1. Slime-filaments on the ventral thallus apex usually 2-celled, the terminal cell subtended by a nearly isodiametric 1-celled stalk cell; midrib cells usually with transverse and vertical

bands of colorless to brownish wall thickening in thallus cross-section; pseudoperianth tubular, but the side toward the apex lower than the back side, generally lying on the thallus surface with the opening toward the thallus apex; pseudoperianth mouth entire to slightly crenulate. . . . . **P. neesiana**

1. Slime-filaments on the ventral thallus apex 3–6-celled (seldom 2-celled), the terminal cell subtended by 2–5 elongate stalk cells; midrib cells without transverse and vertical bands of colorless to brown wall thickening in thallus cross-section; pseudoperianth tubular and erect; pseudoperianth mouth dentate to ciliate. . . . . **P. endiviifolia**

Excluded. Pellia epiphylla (L.) Corda. Frye and Clark (1937) reported *P. epiphylla* for California. However, all herbarium specimens labeled *P. epiphylla* examined in this study were found to be either *P. endiviifolia* or *P. neesiana*. *Pellia epiphylla* could not be confirmed for California. For this monoicous species, look for plants with antheridia and archegonia on the same branch or on separate branches of the same thallus.

Pellia endiviifolia (Dicks.) Dumort.

Distinctive features. This dioicous species often has purplish coloration in the fall. Look for a) slime-filaments 3–6-celled near the apex of the thallus ventral surface, b) mature midrib tissue in thallus cross-section without colorless to brown transverse and vertical bands of secondary wall thickening; and c) erect tubular pseudoperianths with dentate to ciliate mouths.

Separation. This species and *P. neesiana* can grow in close proximity, and occasionally thallus sizes and forms are similar. *Pellia endiviifolia* can be separated by a) slime filaments of 3–6 cells (vs. usually only 2 cells in *P. neesiana*), b) the absence of colorless to brown transverse and vertical bands of wall thickening on cells of mature midrib tissue (vs. transverse and vertical bands of wall thickening usually present: **Caution:** wall thickenings are not always well-developed or present in all thalli of *P. neesiana*), and c) erect tubular pseudoperianths with a dentate to ciliate mouth (vs. pseudoperianths with the side toward the thallus apex lower than the back side, and with an entire to crenulate mouth).

Illustrations. Damsholt 2002; Paton 1999; Schofield 2002; Schuster 1992a; Smith 1990.

Habitat. Shaded creek banks, drainages and seepages in meadows and forests. Elevation from 1400 to 2900 m.

Distribution. Pellia endiviifolia occurs in Europe, Asia, North Africa, and North America. Calif. Geographic Regions: **CR**: Siskiyou Co. *Shevock 26195* (CAS), **KR**: Siskiyou Co. *Doyle 1993* (male) (UC), **MP**: Modoc Co. *Doyle 807* (UC), **SN**: Fresno Co. *Doyle 2463* (female & male) (UC).

P. neesiana (Gottsche) Limpr.

Distinctive features. Look for a) 2-celled slime-filaments on the ventral surface of the apical region, the basal cell of the filament is short and has conspicuous brownish-gray contents, b) mature midrib tissue in thallus cross-section usually with colorless to brown transverse and vertical bands of secondary wall thickening, c) tubular young pseudoperianths with the side away from the thallus apex lower, resulting in what appears to be a pseudoperianth that is prostrate on the thallus with the opening toward the thallus apex, and c) an entire to crenulate pseudoperianth mouth (but older ones can be lacerated).

Separation. Vegetative and male plants of *P. neesiana* can be confused with *P. endiviifolia*. For separation see *P. endiviifolia*.

Illustrations. Damsholt 2002; Paton 1999; Schuster 1992a.

Habitat. Full sun to partial shade; creek banks, drainages, seepages and marshes in meadows and forests. Elevation from near sea-level to 3100 m.

Distribution. Pellia neesiana occurs in Europe, Asia, and North America. Calif. Geographic Regions: **CR**: Tehama Co. *Doyle 9394* (UC), **KR**: Del Norte Co. *Doyle 7730* (female) (UC), **MP**: Modoc Co. *Doyle 11089* (female) (UC), **NC** Mendocino Co. *Bourell 3628* (CAS), **SN**: Plumas Co. *Dillingham 2173* (UC). The *Schallert 210* (NY 263663) collection of *P. neesiana* from **CC**, Big Sur State Park, Monterey Co., was mis-identified; the packet contains a mixture of non-reproductive *Phaeoceros sp.* and *Riccardia chamedryfolia*.

Riccardia Gray 1821
(Aneuraceae)

These thalloid plants are pinnately, palmately or irregularly branched. The thallus has a poorly defined midrib that lacks a central strand of elongate, thick-walled cells. Determination of the number and distribution of oil-bodies in living plants is a great aid in species identification, because of the morphological variability of the vegetative thallus. Oil-bodies are lost on drying; try to keep alive a small sample of your collection for later microscopic examination and keep your notes with the collection.

Four species in California.

Species Key

1. Thallus 1–3 times pinnately branched. . . . . **2.**
1. Thallus palmately or irregularly branched. . . . . **3.**
2. Lateral margins of terminal and secondary branches usually unistratose for 2–4 cells; branches often narrowed toward the apex; oil-bodies usually absent from epidermal and ultimate cells of the lateral margins, but present in internal tissue. . . . . **R. multifida**
2. Lateral margins of terminal and secondary branches unistratose for 1 (seldom more than 2) cells; branches usually narrowed toward the base; oil-bodies usually present in all thallus cells. . . . . **R. chamedryfolia**
3. Thallus irregularly to sub-palmately branched; branches up to 2 mm wide, somewhat broadened at apex; median epidermal cells of dorsal surface 30–60 μm wide × 60–120 μm long; oil-bodies usually lacking in all cells (rarely present in some older internal cells). . . . . **R. latifrons**
3. Thallus palmately branched; branches usually less than 0.5 mm wide, more-or-less parallel sided or slightly narrowed toward apex; median epidermal cells of dorsal surface 16–42 μm wide × 28–56 μm long; oil-bodies usually absent in epidermal cells, but present in internal cells. . . . . **R. palmata**

Riccardia chamedryfolia (With.) Grolle

Distinctive features. These pinnately branched, autoicous plants generally are light-green in shade and occasionally blackish in sun-forms. Look for a) branches usually slightly narrowed toward the branch base, b) branch lateral margins usually of 1 unistratose row of cells (margins of some branches occasionally have 2, rarely more, unistratose rows of cells), c) dorsal epidermis generally with hexagonal cells with thin colorless walls, d) mature median cells of the dorsal epidermis 22–50 μm wide × 55–90 μm long, e) brownish oil-bodies present in nearly all epidermal, marginal and internal cells.

Separation. This species is highly polymorphic and can be confused with *R. latifrons* and *R. multifida*. It is separated from *R. latifrons* by a) irregular 1–3 pinnate branching (vs. usually subpalmate branching in *R. latifrons*), and b) nearly all epidermal cells with oil-bodies (vs. oil-bodies absent in all epidermal cells). *Riccardia chamedryfolia* is separated from *R. multifida* by a) lateral margins of branches usually unistratose for only 1 cell row (vs. branch lateral margins unistratose for 2–4 cell rows in *R. multifida*), b) branches usually narrowed toward the apices (vs. branches narrowed toward the base), and c) oil-bodies present in most epidermal and marginal cells (vs. oil-bodies lacking in most epidermal and marginal cells).

Illustrations. Damsholt 2002; Paton 1999; Schuster 1992a; Smith 1990.

Habitat. Wet rocks, damp soil of banks, decayed wood, and tree roots; generally near, or submersed in dripping, running or slowly moving water. Elevation from near sea-level to 2300 m.

Distribution. Riccardia chamedryfolia occurs in Europe, Asia, and North and South America. Calif. Geographic Regions: **CC**: San Francisco Co. *Shevock 19017* (UC), **CR**: Shasta Co. *Doyle 10991* (UC), **DMoj**: Inyo Co. *Laeger 2623b* (CAS), **KR**: Siskiyou Co. *Doyle 9218* (UC), **NC**: Humboldt Co. *Doyle 11380* (UC), **SN**: Nevada Co. *Doyle 10004* (UC).

Riccardia latifrons (Lindb.) Lindb.

Distinctive features. These autoicous, pale to bright green plants are subpalmately or irregularly branched. Look for a) lateral branches 0.5–1 mm (or more) wide and usually narrowed toward the

base, b) lateral branch margins of 1 cell wide, c) epidermal cells large, 5–6-angled and thin-walled, d) mature median cells of the dorsal epidermis usually 30–54 μm wide × 60–150 μm (or more) long, and e) oil-bodies generally absent in all thallus cells (vs. occasionally present in some older internal thallus cells).

Separation. This species and *R. palmata* grow on decaying logs and stumps, and can be confused. *R. latifrons* is separated from *R. palmata* by a) large dorsal epidermal cells, usually 60–150 μm long × 30–54 μm wide (vs. dorsal epidermal cells 28–56 μm × 16–42 μm in *R. palmata*), b) all dorsal epidermal cells with colorless, thin walls (vs. older dorsal epidermal cells with brownish, equally thickened walls), c) branches 0.5–1 mm (or more) wide and narrowed toward the base (vs. branches less than 0.5 mm wide and not narrowed toward the base), and d) oil-bodies normally absent from epidermal and internal cells (vs. oil-bodies absent in epidermal cells, but present in internal cells). See *R. chamedryfolia* for separation from that species.

Illustrations. Damsholt 2002; Paton 1999; Schofield 2002; Schuster 1992a; Smith 1990.

Habitat. Damp, shaded areas: moist decaying logs; cut ends of tree trunks; soil with moss in seepages; soil at base of wet, shaded cliffs. Elevation from near sea-level to 1825 m; but mostly below 1000 m.

Distribution. Riccardia latifrons occurs in Europe, Asia, North Africa, and North America. Calif. Geographic Regions: **CC**: Monterey Co. *Doyle 6445* (UC), **CR**: Tehama Co. *Doyle 8766A* (UC), **KR**: Trinity Co. *Doyle 8654* (UC), **MP**: Modoc Co. *Doyle 6673* (UC), **NC**: *Norris 85083* (UC), **SN**: Tuolumne Co. *Norris 104020* (UC).

Riccardia multifida (L.) Gray

Distinctive features. These autoicous, green to brownish-green thalloid plants are 2–3-times pinnately branched. Look for a) branches often crowded and mostly narrowed toward the tip, b) margins of ultimate and subterminal branches unistratose for a width of 2–4 cells, giving the branches a translucent appearance, c) dorsal epidermal cells polygonal and with thin colorless walls, d) mature median dorsal epidermal cells 25–40 μm wide and 50–75 μm (or more) long, e) large brownish-gray oil-bodies present in the internal thallus cells, but absent from most epidermal and marginal cells.

Separation. This species usually is easy to identify because of the 2–4 cells wide unistratose lateral margins of ultimate and sub-terminal branches. *Riccardia multifida* occasionally can be confused with the polymorphic *R. chamedryfolia*. See *R. chamedryfolia* for separation from that species.

Illustrations. Damsholt 2002, Paton 1999; Schuster 1992a.

Habitat. Shaded, wet areas; usually on decaying logs and organic matter; also on wet rocks and soil of stream banks. Elevation from near sea-level to 1700 m.

Distribution. Riccardia multifida occurs in Europe, Asia, North Africa, New Zealand, and North America. Calif. Geographic Regions: **CC**: Santa Cruz Co. *Doyle 8872* (UC), **KR**: Trinity Co. *Doyle 6711* (UC), **NC**: Mendocino Co. *Doyle 6278* (sporophytes) (UC), **SN**: Yuba Co. *Doyle 9579* (UC).

Riccardia palmata (Hedw.) Carruth.

Distinctive features. These dioicous plants are pale- to deep-green, becoming brownish or grayish when older. The main axis is prostrate (adhering to substrate), from which arise erect, narrow and rather rigid, simple or palmately-lobed branches. Look for a) branches usually with rounded margins in cross-section, b) equally thick-walled epidermal cells, c) small mature median dorsal epidermal cells usually 16–42 μm wide × 28–56 μm long, and d) 1 or 2 oil-bodies in the internal thallus cells, but mostly absent from the epidermal and marginal cells. Endogenous gemmae often developing near branch apices in such large numbers that the thallus has a light-green, powdery appearance.

Separation. Young plants of this species and *R. latifrons* occasionally grow together on decaying logs and stumps, can be confused in the field; see *R. latifrons* for separation from that species.

Illustrations. Damsholt 2002; Paton 1999; Schuster 1992a; Smith 1990.

Habitat. On shaded, moist decaying logs. Elevation from 100 to 1300 m.

Distribution. Riccardia palmata occurs in Europe, Asia, and North America. Calif. Geographic Regions: **CR**: Tehama Co. *Doyle 11101* (UC), **NC**: Humboldt Co. *Doyle 9007* (UC).

LEAFY LIVERWORTS

Leafy liverworts comprise the largest group of liverworts in California. Distinctive characteristics include a) archegonia developing at the apex of a main stem or lateral branch, resulting in the termination of continued apical growth of that shoot, b) stems with two rows of lateral leaves (a third row of leaves, underleaves, may or may not be present), and c) rhizoids always smooth-walled.

In California, there are 29 genera, 87 species, 6 infraspecific taxa (subspecies/varieties), and 1 species to be described in a subsequent paper. Two genera (*Jamesoniella* and *Pleurocladula*) previously reported for California could not be confirmed, 1 genus (*Herbertus*) is questionable, and 12 species previously reported for California, could not been confirmed.

GENUS KEY (SEE GLOSSARY [APPENDIX I] FOR DEFINITION OF TERMS)

Because many collections will consist only of non-reproductive plants, this key primarily uses vegetative characteristics. Some genera will show in the key more than once because of morphological diversity of species in those genera.

1. Leaves complicate-bilobed (lobes folded 180°; the ventral lobe cylindrical in most species of *Frullania*). . . . . **2.**
1. Leaves unlobed, or bilobed to 4-lobed, but never complicate-bilobed. . . . . **7.**
2. Dorsal lobe larger than the ventral lobe. . . . . **3.**
2. Dorsal lobe slightly to greatly smaller than the ventral lobe. . . . . **5.**
3. Underleaves absent. **Radula**
3. Underleaves present. **4.**
4. Underleaves bilobed. **Frullania**
4. Underleaves entire (not bilobed). . . . . **Porella**
5. Leaf lobes lanceolate, tapering from near the base to an acute or acuminate apex. . **Douinia**
5. Leaf lobes narrowly lingulate or narrowly ovate to reniform, not tapering from near the base to an acute or acuminate apex. . . . . **6.**
6. Shoot tips mostly curving upwards; leaf lobes narrowly lingulate; perianths cylindrical, narrowing to the mouth. . . . . **Diplophyllum**
6. Shoot tips mostly curving downwards; leaf lobes narrowly to broadly ovate to suborbicular or reniform; perianths flattened, wide at the mouth. . . . . **Scapania**
7. Leaves mostly 3–4 lobed. **8.**
7. Leaves unlobed or mostly 2-lobed (occasionally 2 and 3 lobed on the same shoot). . . . . **13.**
8. Leaves deeply divided to (or nearly to) the base; leaf lobes linear. . . . . **9.**
8. Leaves clearly not divided to the base (i.e., with a laminar base); leaf lobes not linear. . . . **10.**
9. Leaves divided into 3 or 4 uniseriate filaments (lobes), to within one cell of the leaf base. **Blepharostoma**
9. Leaves divided into 3 or 4 lobes that are mostly 2 cells wide at the lobe base. . . . . . **Kurzia**
10. Plants yellowish- to reddish-brown; leaf lobe apices and margins with filaments. . . **Ptilidium**
10. Plants green, bluish-green or yellowish-green; leaf lobe apices and margins without filaments. **11.**
11. Leaves incubous (the front margin of a leaf lies <u>over</u> the rear margin of the leaf closer to the stem apex in dorsal view); leaf lobes equal. . . . . **Lepidozia**
11. Leaves succubous (the front margin of a leaf lies <u>under</u> the rear margin of the leaf closer to the stem apex in dorsal view); leaf lobes unequal. . . . . **12.**
12. Underleaves present (observe at shoot apex because of dense rhizoid growth in older stem areas); leaves 3–4-lobed on vegetative stems. . . . . **Barbilophozia**
12. Underleaves absent; leaves all or mostly 2-lobed on vegetative stems. . . . . **Lophozia**
13. Leaves and underleaves of similar size and shape (three rows of more-or-less similar leaves = isophyllous). **14.**
13. Leaves and underleaves, if present, of dissimilar size and shape (two rows of lateral leaves and one row of smaller underleaves = anisophyllous). . . . . **15.**
14. Plants grayish- to whitish-green; leaf cells uniformly thickened without conspicuous trigones; leaf tips appressed to the stem. . . . . **Anthelia**
14. Plants brownish-green to yellowish-brown; leaf cells with bulging trigones; leaf tips spreading. **Herbertus**
15. Leaves incubous (the front margin of a leaf lies <u>over</u> the rear margin of the leaf closer to the stem apex). **16.**

15. Leaves succubous (the front margin of a leaf lies under the rear margin of the leaf closer to the stem apex), or transversely or subtransversely inserted. . . . . **17.**
16. Leaf apices entire or with an apical notch; underleaves bilobed or notched. . . . . **Calypogeia**
16. Leaf apices with 2–4 shallow apical teeth; underleaves with 0–4 shallow teeth. . . . **Bazzania**
17. Leaf apices rounded, truncate, notched, or broadly indented. . . . . **18.**
17. Leaf apices clearly lobed. . . . . **25.**
18. Underleaves present and conspicuous unless obscured by dense rhizoid growth (to minimize problem with rhizoid observation, look at the ventral surface of the stem very near the apex). . . . . **19.**
18. Underleaves absent or small and inconspicuous. . . . . **21.**
19. Rhizoids in tufts mostly surrounding reddish cushions on the ventral stem surface. **Gyrothyra**
19. Rhizoids in tufts from leaf or underleaf bases and/or scattered on the ventral stem surface. **20.**
20. Leaf apices rounded, truncate, slightly notched, or broadly indented; leaves decurrent on the dorsal stem surface; perianths on dwarf branches with modified leaves. . . . **Chiloscyphus**
20. Leaf apices usually shallowly bilobed, at least on some leaves; leaves not or short decurrent on the dorsal stem surface; perianths on main branches with normal leaves.. . . . . (some species of) **Lophocolea**
21. Underleaves present at least near the shoot apex, small. . . . . **22.**
21. Underleaves absent, or very small and ephemeral. . . . . **23.**
22. Median leaf cells 38–50 µm wide × 50–75 µm long; gemmae often on the margins of modified leaves. . . . . **Mylia**
22. Median leaf cells 20–38 µm wide × 25–50 µm long; gemmae absent. . . . . **Nardia**
23. Leaf margin usually toothed or serrate, with the margin away from the shoot apex often reflexed, especially when dry. . . . . **Plagiochila**
23. Leaf margin smooth, not toothed or serrate, with the margin not reflexed. . . . . **24.**
24. Underleaves absent; perianth mouth smooth or toothed. . . . . **Jungermannia**
24. Underleaves very small, often present near the shoot apex; perianth mouth ciliate. **Jamesoniella**
25. Epidermal cells of the stem larger than and forming a differentiated layer (hyalodermis) around the internal cells (the hyalodermis is obvious in dry specimens). . . . . **26.**
25. Epidermal cells of the stem not forming a distinct hyalodermis. . . . . **27.**
26. Underleaves present, distinct. . . . . **Pleurocladula**
26. Underleaves absent. . . . . **Cephalozia**
27. Underleaves present on both vegetative and reproductive stem regions. . . . . **28.**
27. Underleaves absent, scarce, or restricted to reproductive stem regions. . . . . **32.**
28. Underleaves large. . . . . **29.**
28. Underleaves small. . . . . **30.**
29. Underleaves usually with 1 or 2 lateral teeth; rhizoids in tufts from underleaf base; leaf lobes ending in 2–5 superposed cells; plants green to whitish-green, not opaque. . . . . **Lophocolea**
29. Underleaves without lateral teeth; rhizoids from both underleaf base and stem tissue; leaf lobes not ending in 2–5 superposed cells; plants green to yellowish-green, opaque. . **Geocalyx**
30. Plants thin and thread-like, 0.1–0.5 mm wide. . . . . (some species of) **Cephaloziella**
30. Plants not thin and thread-like, 0.6–3.5 mm wide. . . . . **31.**
31. Leaves usually broadly spreading from the stem, seldom concave; underleaves usually with 1 or 2 lateral teeth or thread-like appendages. . . . . (some species of) **Lophozia**
31. Leaves usually erect and concave; underleaves usually without 1 or 2 lateral teeth or thread-like appendages. . . . . (some species of) **Nardia**
32. Leaves closely overlapping and appressed, the stem not visible. . . . . **Gymnomitrion**
32. Leaves often overlapping, but the stem visible in mature shoot areas. . . . . **33.**
33. Leaves bilobed 0.5 or more their length; shoots usually thin and threadlike.. . . . . (some species of) **Cephaloziella**
33. Leaves bilobed mostly less than 0.5 their length; shoots usually not thin and threadlike. **34.**
34. Leaves mostly clearly obliquely inserted. . . . . **35.**
34. Leaves transversely or sub-transversely inserted. . . . . **36.**
35. Leaf lobe apices (of California species) rounded; underleaves absent or small and infrequent; perianth smooth from base to mouth. . . . . **Gymnocolea**
35. Leaf lobe apices acute, underleaves absent; perianth smooth below, but plicate above middle to mouth. . . . . (some species of) **Lophozia**
36. Leaves bilobed with the base of the dorsal and ventral leaf lobes transversely to sub-transversely inserted; dorsal and ventral lobes generally of similar size; perianths short, not exserted above female bracts. . . . . **Marsupella**

36. Leaves bilobed with the base of the dorsal lobe transversely inserted, but base of the ventral lobe obliquely inserted; dorsal lobe slightly smaller than ventral lobe; perianths long exserted above female bracts. . . . . **Anastrophyllum**

Uncertain status. Lophocolea gemmiparous A. Evans. *Thiers 5403a* was identified as *Lophocolea gemmiparous*. However, rhizoids scattered on the stem surface and the nature of the antheridial branch removes the Type specimen (and *Thiers 5403a*) from *Lophocolea* and the Geocalycaceae (P. Davison, personal communication). Additional material would help determine whether "*Lophocolea gemmiparous*" should be included in an existing or a new genus. The California collection site data are: Sierra County; Tahoe National Forest; seasonal stream in meadow along Webber Lake Road; Red fir forest; 6 June 1987; bryophyte cohorts included *Fontinalis antipyretica, Scapania irrigua, Chiloscyphus polyanthos* var. *rivularis*, and *Calypogeia* sp. (B. Thiers, personal communication). It is a high priority to relocate this taxon.

Anastrophyllum (Spruce) Steph. 1893
(Scapaniaceae)

Plants of this genus usually have a) strongly concave and unequally bilobed leaves with the dorsal lobe smaller than the ventral lobe, b) leaf cells with equally thickened walls or strongly bulging and occasionally confluent trigones, and c) stems with no underleaves. Gemma clusters are common at shoot tips.

One species in California.

Anastrophyllum minutum (Schreb.) R. M. Schust.

Distinctive features. These dioicous, dark green to yellowish-brown plants are 0.4–1.5 mm wide and 1–3 cm long. Look for a) unequally bilobed leaves that are strongly concave and in two rows (distichous), b) dorsal leaf lobes smaller than the ventral lobes, c) cells in the leaf lobes in concentric rows, d) median leaf cells 14–24 μm wide and 18–26 μm long, e) leaves that are obliquely inserted ventrally and transversely inserted dorsally, approaching complicate-bilobed in appearance, f) cells in the upper part of the leaf equally thick-walled and without trigones; those in the lower part often with distinct trigones, g) 2–5 oil-bodies per cell, h) underleaves lacking, i) red to reddish-brown clusters of 2–4-celled, angular to knobby gemmae at the apices of erect shoots, and j) perianth mouths lobed and with teeth 1–3 cells long.

Separation. This species is likely to be confused only with small species of *Marsupella*. *Anastrophyllum minutum* has a) lobe cells often in concentric rows (vs. not organized into rows in *Marsupella*), b) asymmetrical leaf lobes (vs. symmetrical leaf lobes) c) gemmae common (vs. gemmae absent), d) hyaline rhizoids (vs. rhizoids usually with some pigmentation), and e) 2–5 oil-bodies per cell (vs. usually only 2 large oil-bodies per cell).

Illustrations. Damsholt 2002; Paton 1999; Schofield 2002; Schuster 1969.

Habitat. Damp, dimly-lit soil and rock habitats, e.g., base of dripping cliffs and seeps; in deep crevices below massive overhanging ledges. Elevation over 1200 m.

Distribution. Anastrophyllum minutum occurs in Europe and North America. Calif. Geographic Regions: **KR**: Del Norte Co. *Jessup 7408* (SOC).

Anthelia (Dumort.) Dumort. 1835
(Antheliaceae)

This is a distinctive, easily recognized genus of higher elevations. Leaves and underleaves a) are similar in size and form (isophyllous) and transversely inserted, b) overlap each other, appearing 3-ranked and tightly appressed to the stem, and c) are deeply bilobed, the lobes narrow and with acute apices. Oil-bodies are absent from all cells. When dry, plants in mats and large cushions often are conspicuously covered with what appears to be fungal hyphae, but is whitish material formed by the plants.

One species in California.

Anthelia juratzkana (Limpr.) Trevis.

Distinctive features. These paroicous plants often occur in compact grayish-green or bluish-gray or whitish-gray mats. Shoots usually are 2–7 (rarely over 12) mm long. Look for a) in the field, mats covered

with a whitish substance, b) rhizoids usually present on both main and side branches, c) wide ovate perianths common, each emergent less than 0.5 its length above the bracts, d) elaters with 2–4 thickened helical bands, each band less than 3 μm wide, and e) spores 15–21 μm in maximum diameter.

Separation. This distinctive liverwort is likely to be confused only with young and non-reproductive plants of *Anthelia julacea* (a species not confirmed, but possible, for California). Young plants of the two species can be nearly impossible to separate. *Anthelia juratzkana* usually can be separated by a) shoots generally less than 7 mm long (vs. up to 35 mm long in *A. julacea*), b) thallus color of grayish-green or bluish-gray (vs. yellowish-green or green, often with a brownish coloration), c) paroicous (vs. dioicous), d) wide ovate perianths emergent less than 0.5 their length beyond the bracts (vs. narrowly ovoid perianths emergent by 0.5 or more their length beyond the bracts), e) elaters with 2–4 thickened helical bands, each band less than 3 μm wide (vs. elaters with 2 helical bands, each band 3.5–4.0 μm wide) and f) spores 15–21 μm in diameter (vs. spores 12–16 μm in *A. julacea*).

Illustrations. Damsholt 2002; Paton 1999; Schuster 1974; Smith 1990.

Habitat. Banks of drainages and on hummocks in meadows, and banks and margins of lakes, seepages and creeks. Elevation from 2700 to 3725 m.

Distribution. Anthelia juratzkana is widespread in the arctic-alpine zones of Europe, Asia, North and South America, and New Zealand. Calif. Geographic Regions: **CR**: Shasta Co. *Doyle 9829* (perianths) (UC), **SN**: Fresno Co. *Shevock 13864* (CAS).

Excluded. Anthelia julacea (L.) Dumort. Based on *Howell 584 & 585* (CAS), Sutliffe (1942, 1947) reported the presence of *A. julacea* from the high Sierra Nevada of Madera County. Both Howell collections, however, are *A. juratzkana*, as were other California collections of *Anthelia* examined in this study. *A. julacea* could not be confirmed for California but is expected.

Barbilophozia Loeske 1907
(Scapaniaceae)

Distinctive features of the genus include a) leaves that usually are 3–4-lobed (occasionally 2–3-lobed in some species), and b) usually conspicuous, deeply bifid underleaves often with filaments on the margins.

One species confirmed for California.

Barbilophozia hatcheri (A. Evans) Loeske

Distinctive features. These green to yellowish-brown plants usually are 1.5–2.8 mm wide and 2–4 cm long. Look for a) leaves 3–4-lobed, b) leaf lobes mostly straight-sided and often with apiculate apices of 1–2 (or 3) rather short, thick-walled cells, c) leaves slightly decurrent on the dorsal stem surface, d) leaf base on the ventral stem surface with 1–3 (occasionally up to 5) multicellular filaments, e) large bilobed underleaves with numerous, contorted multicellular filaments on the margins, and f) brownish-red gemmae, angular and 1–2-celled, usually present on lobe apices and leaf margins (older leaf margins often are erose because of gemmae development).

Separation. The combination of leaves 3–4 lobed, large bilobed underleaves with numerous multicellular marginal filaments, and angular brownish-red gemmae separates *B. hatcheri* from the other species of *Barbilophozia*, and from species of *Lophozia*.

Illustrations. Damsholt 2002; Paton 1999; Schuster 1969; Smith 1990.

Habitat. On shaded soil of rocky banks, slopes and cliffs, and on organic matter. Elevation from 1400 to 3665 m.

Distribution. Barbilophozia hatcheri occurs in Europe, Asia, Antarctica, and North and South America. Calif. Geographic Regions: **CR**: Siskiyou Co. *Harling WCH221* (UC), **KR**: Siskiyou Co. *Doyle 5991* (UC), **SN**: Inyo Co. *Doyle 6021* (UC).

Bazzania Gray 1821
(Lepidoziaceae)

Species of this genus have a) asymmetric leaves with incubous insertion, b) leaf apices that are shallowly, sometimes obscurely, lobed or toothed, c) underleaves entire or with 1–4 shallow apical

lobes or teeth, and d) flagelliform branches arising from the axils of the underleaves and downwardly directed.

One species in California.

Bazzania denudata (Torr. ex Gottsche, Lindenb. and Nees) Trevis.

Note. This species distinctively has stem areas devoid of leaves. However, the extent of leaf loss is highly variable, even within a single population. For example a) many leaves on some stems are deciduous (caducous), or b) all leaves persist on some stems, or c) some stems have short denuded regions, separated by long regions with persistent leaves. Look at more than one shoot during identification.

Distinctive features. Living plants are light green to green. Look for a) short or long stem areas devoid of leaves, b) highly variable leaf apices, even on the same stem, the leaf apex can gradually taper to an obtuse point, or be broad and rounded, or be truncate, c) leaf apices usually with 1–3 blunt teeth, but varies from 0 to 4 teeth, d) median leaf cells 10–30 μm wide and 23–36 μm long, e) underleaves about twice as wide as the stem, f) broad and truncate apices of underleaves with with 0–4 shallow lobes or teeth, and g) five or more oil-bodies per cell.

Separation. Bazzania denudata should not be confused with any other California leafy liverwort.

Illustrations. Schofield 2002; Schuster 1969.

Habitat. On moist, shaded decaying logs in redwood forests; near sea-level to 30 m.

Distribution. Bazzania denudata is widely distributed in North America. Calif. Geographic Regions: **KR**: Del Norte Co. *Doyle 11041* (UC), **NC**: Humboldt Co. *Doyle 10955* (UC).

Excluded. Bazzania tricrenata (Wahlenb.) Lindb. The report by Clark and Frye (1936) of *B. tricrenata* from near Crescent City, Del Norte County was based on the mis-identification of *Frye 139* (WTU); this specimen is *Calypogeia fissa* subsp. *neogaea*. Also *Branscomb 22373* (WTU) was mis-identified as *B. tricrenata*; this specimen is *Calypogeia muelleriana*. No herbarium specimen examined in this study confirmed this species in California; however *Norris 52921* (DUKE) cited by Hong (1988) was not studied.

Blepharostoma (Dumort.) Dumort. 1835
(Pseudolepicolaceae)

Species of *Blepharostoma* can hardly be confused with any other California liverwort. Distinctive are leaves and underleaves divided to the base into 2–4 uniseriate filaments.

Two species in California.

Species Key

1. Lateral leaves and underleaves divided to base into 3–4 uniseriate filaments; leaf filaments unbranched; transverse walls of leaf filaments usually slightly bulging outwards in profile. . . . . **B. trichophyllum**
2. Lateral leaves and underleaves divided to base into 2–3 uniseriate filaments; leaf filaments occasionally once-branched 2–4 cells above leaf base; transverse walls of leaf filaments slightly depressed or smooth in profile. . . . . **B. arachnoideum**

Blepharostoma arachnoideum M. Howe

Additional field-work is needed to better understand the distribution and reproduction of this seldom collected species. Culture-studies in the laboratory are needed to a) try to induce sexual reproductive structures and b) compare growth and morphology of this species with that of *B. trichophyllum* when both are grown under identical environmental conditions. Molecular studies are needed to assess the degree of relatedness of *B. arachnoideum* and *B. trichophyllum*.

Distinctive features. The grayish-green shoots of this species are easily overlooked; they occur in small patches and often grow intermixed with other bryophytes. Look for a) leaves and underleaves divided nearly to the base into 2–3 uniseriate filaments, some leaf filaments are once-branched 2–4 cells above the leaf base, b) transverse walls of the leaf and underleaf filaments not thickened at the

juncture of lateral walls, the walls appear slightly depressed, seldom smooth in profile, c) stem epidermal cells 23–60 μm wide × 50–150 μm long, and d) unicellular gemmae common, the terminal cell of a filament dividing conidia-like forming a chain of small unicellular gemmae. Sexual reproduction is not known.

Separation. See *B. trichophyllum* for separation of these two species.

Illustrations. Clark and Frye 1928.

Habitat. Shaded, damp decaying logs, and soil and rocks of creek-banks. Elevation from 15 to 1600 m.

Distribution. Blepharostoma arachnoideum is endemic to the Pacific Coast of North America. Calif. Geographic Regions: **KR**: Siskiyou Co. *Doyle 11072* (UC), **NC**: Humboldt Co. *Doyle 10579* (UC).

Blepharostoma trichophyllum (L.) Dumort.

Distinctive features. Shoots of this species usually occur in pale- to yellowish-green patches. Look for a) leaves divided nearly to the base into 3–4 unbranched, uniseriate filaments and underleaves divided nearly to the base into 2–4 unbranched, uniseriate filaments, b) cells of leaves and underleaves with evenly thickened walls without trigones, c) transverse cell walls of leaf and underleaf filaments usually thickened outwardly, appearing as a bulge, but occasionally smooth in profile, d) stem epidermal cells 15–38 μm wide and 28–95 μm long, e) perianths common, mouth ciliate, and f) unicellular gemmae not common.

Separation. Blepharostoma trichophyllum is separated from *B. arachnoideum* by a) leaves that are divided into 3–4 uniseriate lobes (vs. 2–3 lobes in *B. arachnoideum*), b) unbranched uniseriate leaf lobes (vs. uniseriate leaf lobes occasionally branched 2–4 cells from the base), c) transverse walls of filament usually thickened outwardly, appearing as bulges in profile (vs. transverse walls unthickened, appearing slightly indented or smooth in profile, d) smaller stem epidermal cells, generally 15–38 μm wide and 28–95 μm long (vs. stem epidermal cells 23–60 μm wide and 50–150 μm long, and e) perianths frequently present (vs. perianths not known).

Illustrations. Damsholt 2002; Paton 1999; Schofield 2002; Schuster 1966; Smith 1990.

Habitat. Shaded wet rocks, soil and decaying wood; banks of creeks, lakes, and depressions; margins of seepages. Elevation from 25 to 3850 m.

Distribution. Blepharostoma trichophyllum occurs in Europe, Asia, and North, Central, and South America. Calif. Geographic Regions: **CC**: Santa Cruz Co. *Kellman 345* (CAS), **CR**: Tehama Co. *Doyle 11103* (UC), **KR**: Siskiyou Co. *Norris 105072* (UC), **NC**: Humboldt Co. *Doyle 10634* (perianths) (UC), **SN**: Fresno Co. *Shevock 17448* (CAS).

Calypogeia Raddi 1818
Calypogeiaceae

Species in this genus have incubous and obliquely inserted leaves. An important aid in the field identification of the genus is the presence of conspicuous clusters of gemmae at the apices of erect specialized shoots. Some plants in a population almost always have gemma-bearing shoots. Also look for a) well-developed underleaves, b) the presence of rhizoids from a specific region, the rhizoid-initial area, at the abaxial base of the underleaves, and c) the development of sporophytes in a colorless and usually subterranean pouch, called a marsupium.

Note. At times, species of this genus can be difficult to identify. Whenever possible, use living plants to note oil-body color (bluish, grayish or colorless) and distribution (e.g., presence or absence in cells of the leaf middle). Keep these data with the herbarium specimen. Also examine mature regions of several healthy shoots (i.e., not immature or etiolated regions of shoots). Some species of the genus (e.g., *C. muelleriana*) exhibit great morphological variation and species identification sometimes can be determined only with use of a combination of characters from mature, healthy plants.

Five species and 1 subspecies in California.

Species Key

1. Oil-bodies distinctly blue in living plants (begin key at 2 for dry plants). . . . . . . **C. azurea**

1. Oil-bodies colorless to grayish in living plants; oil-bodies absent in dry plants. . . . . **2.**
2. Underleaf apices rounded, truncate, shallowly notched, or divided to within 7–14 cells of the rhizoid-initial area. . . . . **3.**
2. Underleaf apices clearly and deeply divided to within 1–6 cells of the rhizoid-initial area. **4.**
3. Healthy mature plants 0.8–2.5 mm wide; many to most marginal cells of leaf tangentially elongate, usually forming a distinct border; marginal cells at leaf apex usually tangentially elongate; narrow transverse rhizoid-initial area, 3–4 × as wide as high; oil-bodies absent from cells in leaf middle. . . . . **C. neesiana**
3. Healthy mature plants usually 2.4–3.2 mm wide; leaf margin with both isodiametric and tangentially elongate cells, forming a discontinous, indistinct border; marginal cells at leaf apex usually isodiametric; rhizoid-initial area transversely oval to nearly round, less than 2× as wide as high; oil-bodies normally present in all cells of the leaf. . . . . **C. integristipula**
4. Mature healthy shoots usually less than 2 mm wide; median leaf cells 24–32 × 28–42 μm, with small, often slightly bulging trigones. . . . . **C. suecica**
4. Mature healthy shoots usually more than 2 mm wide; median leaf cells 32–45 × 24–70 μm, trigones lacking. . . . . **5.**
5. Leaf apices apiculate, acute or bidentate; underleaf divided 1–2 cells from sinus to rhizoid-initial area. . . . . **6.**
5. Leaf apices usually rounded or obtuse, seldom apiculate, acute or bidentate; underleaf divided 2–6 cells to rhizoid-initial area. . . . . **7.**
6. All or most leaves on well-developed stems strongly bidentate; spores more than 14 μm in maximum diameter. . . . . **C. fissa** subsp. **fissa**
6. Most leaves on well-developed stems mostly acute or apiculate, occasionally some, but not most on a stem bidentate; spores less than 14 μm in diameter. . . . . . **C. fissa** subsp. **neogaea**
7. Underleaf lobe apices usually obtuse or rounded, with rounded lateral margins (rarely with teeth or angulations); underleaf divided to within 3–6 cells of the rhizoid-initial area; rhizoid-initial area narrow, strongly transverse. . . . . **C. muelleriana**
7. Underleaf lobe apices acute to subacute, lateral margins occasionally with a blunt tooth, otherwise rounded; underleaf divided to within 2–4 cells of the rhizoid-initial area; rhizoid-initial area transversely oval to nearly round. . . . . **C. azurea**

Excluded. Calypogeia fissa (L.) Raddi subsp. *fissa*. Hong (1990) reported subsp. *fissa* for the Klamath Ranges and Central Coast Region, but cited no specimen. Most or all leaves of this subspecies of *C. fissa* have strongly bidentate apices. During this study, no herbarium specimen was located that had shoots with most or all leaves with strongly bidentate apices. In most California populations, many shoots have a few to several leaves with bidentate leaf apices, which is typical of the subspecies *neogaea*, but never most shoots with strongly bidentate apices, which is typical for subsp. *fissa*. Although left in the key for comparison, *Calypogeia fissa* subsp. *fissa* could not be confirmed for California (see Damsholt 2002, Paton 1999 or Schuster 1969 for illustrations).

2) *Calypogeia suecica* (Arnell and J. Perss.) Müll. Frib. Based on *Frye s.n.*, July 30, 1933 (WTU), Clark and Frye (1936) reported this species for California. Examination during this study indicated that the WTU collection consists of small plants of *C. fissa* subsp. *neogaea* (growing on burned wood, or charcoal). Although Hong (1990) did not list California in the distribution of this species in western North America, he showed two northwestern California and one Sierra Nevada sites in his Figure 3. No herbarium specimens of *C. suecica* were located during this study; it could not be confirmed for California. This species is retained in the key because it likely occurs in the state. Look for *C. suecica* on decaying logs (see Damsholt 2002; Paton 1999; Schuster 1969 for illustrations).

Calypogeia azurea Stotler & Crotz

Distinctive features. Living plants of this species are slightly aromatic and readily identified by the presence of pale to deep blue oil bodies that generally occur in all leaf, underleaf and stem epidermal cells. Although the cell walls of dry shoot apices can have a bluish tint for a variable time, the color quickly disappears in California plants. Examine your specimens while they are still fresh.

With dry plants look for a) subacute, rounded or obtuse leaf apices (occasionally one or more leaf apices on some stems can be acute or bidentate), b) leaf cells with thin to moderately thick walls, c) bilobed underleaves with subacute, triangular or lanceolate lobes; *Doyle 9822* (UC) from Shasta Co. occasionally has trifid underleaves, d) underleaf lobe margins usually round, but occasionally with a blunt tooth on one or both margins, and e) underleaves divided to within 2–4 cells of the rhizoid-initial area.

Separation. *Calypogeia azurea* is morphologically variable and some long-dried specimens can be virtually impossible to separate from *C. muelleriana* and *C. fissa*. Details of leaf and underleaf morphology usually can be used to separate dry plants of *C. azurea* from these two species. Generally, *C. azurea* can be separated from *C. fissa* by a) leaf apices subacute, rounded or obtuse (vs. leaf apices acute or bidentate in *C. fissa*), and b) underleaves divided within 2–4 cells from the rhizoid-initial area (vs. underleaves divided within 1–2 cells from the rhizoid-initial area). *Calypogeia azurea* usually can be separated from *C. muelleriana* by a) underleaves divided within 2–4 cells from the rhizoid-initial area (vs. underleaves usually divided within 4–6 cells from the rhizoid-initial area in *C. muelleriana*), and b) underleaves usually with acute to subacute sinuses and acute to obtuse lobe apices (vs. underleaves usually with obtuse to rounded sinuses and obtuse to rounded lobe apices).

Illustrations. Damsholt 2002; Paton 1999; Schuster 1969; Smith 1990.

Habitat. Damp, shaded decaying logs and organic rich soil near the coast; shaded peaty soil on stream banks and edges of seepages and drainages in the mountains. Elevation from near sea-level to 2965 m.

Distribution. *Calypogeia azurea* occurs in Europe, Asia, North Africa, and North America. Calif. Geographic Regions: **CR**: Tehama Co. *Doyle 9411* (UC) **KR**: Trinity Co. *Doyle 9358* (UC), **MP**: Modoc Co. *Doyle 8638* (UC), **NC**: Humboldt Co. *Doyle 9004* (UC), **SN**: Alpine Co. *Doyle 10797* (UC).

Calypogeia fissa (L.) Raddi subsp. **neogaea** R. M. Schust.

Distinctive features. Look for the following in these grayish- to whitish- to pale-green plants: a) leaves usually with acute, apiculate or bidentate apices (occasionally some shoots in a population will have a few to several [but never most] bidentate leaves, while other shoots in the same population will have few to no bidentate leaves. Carefully examine the population, not selectively only one or two shoots), b) underleaves deeply bilobed to within 1–2 cells of the rhizoid-initial area, and c) underleaves frequently with a blunt tooth on one or both margins.

Separation. *Calypogeia fissa* subsp. *neogaea* can be confused with some forms of *C. muelleriana* (e.g., forms of *C. muelleriana* from the western slope of the Sierra Nevada that approach what Schuster [1969] called subsp. *blomquistii*). *Calypogeia fissa* subsp. *neogaea* usually can be separated from *C. muelleriana* by a) leaf apices acute, apiculate or bidentate (vs. leaf apices usually narrowly rounded in *C. muelleriana*), b) underleaves divided within 1–2 cells of the rhizoid-initial area (vs. underleaves usually divided within 4–6 cells of the rhizoid-initial area), and c) a blunt tooth on one or both underleaf margins (vs. underleaf margins usually smooth and rounded).

Illustrations. Schuster 1969.

Habitat. Shaded silty and sandy mineral soil of hillsides, paths and roads; less often on decaying logs and other organic matter. Elevation from near sea-level to 1625 m, but more common below 1000 m.

Distribution. *Calypogeia fissa* subsp. *neogaea* is North American in distribution. Calif. Geographic Regions: **CC**: Monterey Co. *Kellman 3035* (CAS), **KR**: Trinity Co. *Doyle 8550* (UC), **NC**: Humboldt Co. *Doyle 10632* (UC), **SN**: Yuba Co. *Doyle 9580*.

Calypogeia integristipula Steph.

Distinctive features. In California, these are high elevation plants. Look for a) underleaves large, nearly circular, with round, truncate or notched apices, and divided to within 7–14 cells of the rhizoid-initial area, b) marginal leaf cells mostly isodiametric, but with isolated or occasional series of 2–4 tangentially elongate cells, but not forming a distinct border, c) oil bodies in all leaf cells, and d) a rhizoid-initial area transversely oval to nearly round.

Separation. *Calypogeia integristipula* can be confused with *C. neesiana*. Both species have underleaf apices that are round, truncate or notched, and have highly variable leaf and underleaf size and shape. Oil-body distribution in living plants is the simplest way to separate these two species. *Calypogeia integristipula* has oil-bodies in all leaf cells (vs. oil-bodies absent from cells of the leaf middle in *C. neesiana*). For dry plants without oil-bodies, *C. integristipula* often has 1–4 tangentially elongate marginal leaf cells separated by a varable number of isodiametric cells, and usually has isodiametric cells at the leaf apices (vs. leaves with tangentially elongate marginal and apical cells forming a distinct [but occasionally incomplete] border in *C. neesiana*). Some populations of *C. integristipula*, especially

those with notched underleaves, superficially can be confused with *C. muelleriana*. *Calypogeia integristipula* can be separated by the a) underleaves truncate or notched to within 7–14 cells of the rhizoid-initial area (vs. underleaves distinctly bilobed to within 2–6 cells of the rhizoid-initial area in *C. muelleriana*), and b) presence in leaves of some tangentially elongate marginal cells (vs. usual absence of tangentially elongate leaf marginal cells).

Illustrations. Damsholt 2002; Paton 1999; Schuster 1969; Smith 1990.

Habitat. On peaty soil; shaded creek banks and margins of seepages. Elevation from 2540 to 3212 m.

Distribution. Calypogeia integristipula occurs in Europe and North America. Calif. Geographic Regions: **SN**: Fresno Co. *Doyle 10198* (UC).

Calypogeia muelleriana (Schiffn.) Müll. Frib.

Distinctive features. Plants are green to yellowish- to whitish-green and usually shiny when dry. Look for a) leaves generally heart-shaped with rounded apices, b) large median leaf cells 32–45 μm wide and 45–70 μm long, c) underleaves distinctly bilobed with obtuse to rounded lobe tips, d) underleaves usually divided within 4–6 cells of the rhizoid-initial area, and e) a narrow, transverse rhizoid-initial field.

Separation. This species is morphologically variable and often exists in forms that appear intermediate with other species (see Schuster, 1969, for a discussion of variation within this species). It can be confused with *C. azurea*, *C. fissa* and *C. integristipula*. A suite of characters often must be used to decide species identification. *Calypogeia muelleriana* can be separated from *C. azurea* by a) colorless oil-bodies (vs. blue oil-bodies in *C. azurea*), b) usually heart-shaped leaves (vs. leaves usually wide-ovate), and c) underleaf lobes usually with obtuse or rounded sinuses (vs. sinuses usually acute to subacute). *Calypogeia muelleriana* can be separated from *C. fissa* by a) usually heart-shaped leaves, about as wide as long (vs. oblong-ovate leaves, longer than wide in *C. fissa*), b) leaves with broadly- to narrowly-rounded apices (vs. leaf apices acute, apiculate or bidentate), and c) underleaf lateral margin rarely with a blunt tooth (vs. underleaf margin usually with one or two blunt teeth). *Calypogeia muelleriana* can be separated from *C. integristipula* by a) shiny texture of dry plants (vs. generally dull texture in *C. integristipula*), b) leaves usually heart-shaped, about as wide as long (vs. leaves narrowly ovate, as wide as or longer than wide), and c) underleaves distinctly bilobed, divided to within 4–6 cells of the rhizoid-initial area (vs. underleaves entire or notched, divided to within 7–14 cells of the rhizoid-initial area).

Illustrations. Damsholt 2002; Paton 1999; Schofield 2002; Schuster 1969.

Habitat. On shaded, damp decaying logs; also on soil rich in organic matter; near sea-level to 2900 m, but mostly below 1800 m.

Distribution. Calypogeia mulleriana occurs in Europe, Asia, and North America. Calif. Geographic Regions: **CC**: San Mateo Co. *Doyle 10403* (UC), **CR**: Shasta Co. *Doyle 8752* (UC), **KR**: Trinity Co. *Doyle 9362* (UC), **MP**: Modoc Co. *Doyle 9650* (UC), **NC**: Humboldt Co. *Doyle 10562* (UC), **SN**: Fresno Co. *Laeger 1683* (CAS).

Calypogeia neesiana (C. Massal. and Carestia) Müll Frib.

Distinctive features. Shoots of this species usually are opaque and grayish-green when living, and a glaucous gray-green when dry. Look for a) large nearly circular underleaves with round to notched apices, b) marginal cells of leaves mostly tangentially elongate, forming a distinct border, and c) oil-bodies typically absent from the median leaf cells, but present in the surrounding cells, including the leaf base.

Separation. Calypogeia neesiana has been confused with *C. integristipula*. See *C. integristipula* for separation.

Illustrations. Damsholt 2002; Paton 1999; Schuster 1969; Smith 1990.

Habitat. On shaded soil of creek banks. Elevation from 100 to 210 m.

Distribution. Calypogeia neesiana occurs in Europe, Asia, and North America. Calif. Geographic Regions: **NC**: Humboldt Co. *Doyle 10583* (UC).

Cephalozia (Dumort.) Dumort. 1835
(Cephaloziaceae)

For this genus, look for a) stems generally with large, usually translucent epidermal cells (=hyalodermis) b) succubous bifid leaves, c) underleaves usually absent (occasionally present or restricted to certain areas in a few species), d) unicellular gemmae, and e) oil-bodies absent. Mature, well-developed plants generally are readily identified to species; however, young or etiolated shoots can make identification challenging.

Cephalozia is separated from *Cephaloziella* by a) large, usually translucent stem hyalodermis (vs. hyalodermis lacking in *Cephaloziella*), b) 1-celled gemmae (vs. 2-celled gemmae), c) absence of underleaves (vs. underleaves present in many species), and d) oil-bodies absent in leaf cells (vs. oil-bodies present in leaf cells).

Four species plus two subspecies in California; one species excluded.

Species Key

1. Leaves transversely or sub-transversely inserted on stem; leaves not decurrent on the dorsal stem surface; leaves divided 0.5–0.7 their length; leaf insertion on the dorsal surface of mature stem to, or slightly beyond the midline. . . . . **2.**
1. Leaves obliquely to nearly horizontally inserted on stem; leaves short or long decurrent on the dorsal stem surface; leaves divided 0.25–0.5 their length; leaf insertion on the dorsal surface of mature stem clearly not to the midline. . . . . **4.**
2. Dorsal epidermal cells of mature stem 12–25 µm wide × 20–36 µm long; leaves about as long as wide; cells at base of leaf lobes small, 14–26 µm wide × 16–40 µm long. . . . . **C. bicuspidata** subsp. **ambigua**
2. Dorsal epidermal cells of mature stem 25–60 µm wide × 35–82 µm long or longer; leaves longer than wide; cells at base of leaf lobes 23–54 µm wide × 35–82 µm long or longer. . **3.**
3. Stem dorsal epidermal cells 25–46 µm wide × 40–80 µm long (or longer); cells at base of leaf lobes usually 23–45 µm wide × 35–54 µm long; stolons frequently present. . . . . **C. bicuspidata** subsp. **bicuspidata**
3. Stem dorsal epidermal cells 30–60 µm wide × 60–160 µm long; cells at base of leaf lobes 30–54 µm wide × 40–82 µm long or longer; stolons rare or lacking.. . . . . **C. bicuspidata** subsp. **lammersiana**
4. Leaves strongly decurrent; leaf lobe apices usually clearly connivent. . . . . **5.**
4. Leaves not, or only shortly decurrent; leaf lobe apices not, or only weakly connivent. . . . **6.**
5. Leaves nearly horizontally inserted; cells at base of leaf lobes 30–56 µm wide × 41–75 µm long (or longer); perianth mouth lobed and laciniate, with lacinae ending with 2–6 uniseriate cells. . . . . **C. connivens**
5. Leaves obliquely inserted; cells at base of leaf lobes 20–35 µm wide × 26–42 µm long; perianth mouth crenate-dentate, usually with 1 elongate cell. . . . . **C. lunulifolia**
6. Plants rather large; dorsal cortical cells of stem over 35 µm wide; leaves conspicuously concave; leaf cells usually thin-walled, at base of lobes 28–36 µm wide (or wider) × 33–50 µm long (or longer); perianth mouth crenate-dentate. . . . . **C. pleniceps**
6. Plants smaller; dorsal cortical cells about 15–25 µm wide; leaves only slightly concave; leaf cells usually thick-walled, at base of lobes 15–21 µm wide and 16–25 µm long; perianth mouth ciliate. . . . . **C. catenulata**

Excluded. Cephalozia catenulata (Huebener) Lindb. Hong (1988b) reported this species for California; Fig 6 showed a collection north of San Francisco Bay (**NC**). However, no herbarium specimen was located with the combination of features definitive for *C. catenulata*. Although retained in the key, *C. catenulata* could not be confirmed for California. See Damsholt (2002) and Paton (1999) for description and illustration of this species.

Cephalozia bicuspidata (L.) Dumort.

Three subspecies occur in California. Because of morphological variability, Schuster (1974) reported that chromosome number is the surest method to identify the three subspecies: subsp. *ambigua* has 9 chromosomes, subsp. *bicuspidata* has 18 chromosomes, and subsp. *lammersiana* has 27 chromosomes. Determination of chromosome number is not an option in most cases. Some authors (e.g., Damsholt, 2002; Paton 1999) treat *lammersiana* as a variety of *C. bicuspidata* subsp. *bicuspidata*; some authors (e.g., Paton 1999) treat *ambigua* as a separate species of *Cephalozia*. Robust mature plants of the three

readily can be separated by morphological features and here are treated as three subspecies of *C. bicuspidata.* Measurement of the width and length of dorsal epidermal cells **from several different stems** usually is a good way to separate the three subspecies.

Cephalozia bicuspidata (L.) Dumort. subsp. **bicuspidata**

Distinctive features. This autoicous pale-green to dark-green to yellowish-brown subspecies morphologically is highly variable. When growing on shaded decaying logs, shoots of this species can be large and pale-green, with large leaves and leaf lobes, and thin to moderately thickened cell walls: these plants approach those of subsp. *lammersiana.* In sunny exposed meadow areas of the high Sierra Nevada, the shoots can be small and reddish- to golden-brown, with small leaves and leaf lobes, and thickened cell walls: these plants approach those of subsp. *ambigua.* Look for a) stem dorsal epidermal cells mostly 25–46 μm wide × 40–80 μm long (or longer), b) slight to distinctly concave leaves, c) cells at leaf lobe base mostly 23–45 μm wide × 35–54 μm long (or occasionally longer), d) no underleaves, and e) a perianth mouth with 1–3-celled teeth.

Separation. For separation of this subspecies with subsp. *ambigua*, see under that subspecies. Large growth forms of subsp. *bicuspidata* can be difficult to separate from subsp. *lammersiana*. Typical forms of subsp. *bicuspidata* are separated by a) stem dorsal epidermal cells mostly 25–46 μm wide × 40–80 μm long (vs. stem dorsal epidermal cells 30–60 μm wide × 60–160 μm long in subsp. *lammersiana*), b) cells at the leaf lobe base generally 25–40 μm wide × 35–54 μm long (vs. cells at the leaf lobe base 30–54 μm wide × 40–82 μm long or longer), and c) absence of underleaves (vs. infrequent presence of underleaves near the shoot apex).

Illustrations. Damsholt 2002; Paton 1999; Schuster 1974.

Habitat. Shaded soil of damp, slow to dry habitats, such as decaying logs, peaty soil and mineral soil. Elevation from near sea-level to 3173 m.

Distribution. Cephalozia bicuspidata subsp. *bicuspidata* occurs in Europe, Asia, and North America. Calif. Geographic Regions: **CC**: Santa Cruz Co. *Kellman 406* (CAS), **CR**: Lassen Co. *Doyle 9799* (UC), **KR**: Del Norte Co. *Doyle 10597* (UC), **MP**: Modoc Co. *Doyle 8642* (UC), **NC**: Humboldt Co. *Doyle 10996* (UC), **SN**: Fresno Co. *Shevock 17448* (CAS).

Cephalozia bicuspidata (L.) Dumort. subsp. **ambigua** (C. Massal.) R. M. Schust.

Distinctive features. For this autoicous yellowish-, greenish-, to grayish-green subspecies, look for a) small shoots less than 0.6 mm wide × up to 1.5 cm long, b) stem dorsal epidermal cells mostly 12–25 μm wide × 20–36 μm long, c) leaves nearly transversely inserted, d) leaf cells mostly with thick brownish walls, e) cells at the leaf lobe base 14–26 μm wide × 16–40 μm long, f) occasional presence of subulate underleaves near the shoot apex, and g) a perianth mouth with 1-celled teeth.

Separation. Some growth forms of *C. bicuspidata* subsp. *ambigua* are difficult to impossible to distinguish from some high elevation forms of *C. bicuspidata* subsp. *bicuspidata*. Typical forms of *C. bicuspidata* subsp. *ambigua* are separated by a) narrower stem dorsal epidermal cells, 12–25 μm wide (vs. stem dorsal epidermal cells 25–46 μm wide in *C. bicuspidata* subsp. *bicuspidata*) and b) smaller cells at the leaf lobe base 14–26 μm wide × 16–35 μm long (vs. cells at the leaf lobe base usually 23–45 μm × 35–54 μm).

Illustrations. Damsholt 2002; Paton 1999; Schuster 1974.

Habitat. On damp to wet usually peaty soil in high elevations; especially banks of drainages in meadows, marshes and seepages. Elevation from 2700 to 3000 m.

Distribution. Cephalozia bicuspidata subsp. *ambigua* occurs in Europe, Asia, and North America. Calif. Geographic Regions: **SN**: Tuolumne Co. *Doyle 11191* (UC).

Cephalozia bicuspidata (L.) Dumort. subsp. **lammersiana** (Huebener) R. M. Schust.

Distinctive features. This autoicous whitish- to pale-green subspecies is the largest of the three subspecies of *C bicuspidata*. Look for a) stem dorsal epidermal cells 30–60 μm wide × 60–160 μm long, b) cells at the leaf lobe base 30–54 μm wide × 40–82 μm long, c) lingulate to subulate underleaves infrequently present near the shoot apex, and d) a perianth mouth with teeth 2–5 cells long.

Separation. Subspecies *lammersiana* and larger growth forms of subsp. *bicuspidata* often can be difficult to separate. See *C. bicuspidata* subsp. *bicuspidata* for separation from that subspecies.

Illustrations. Damsholt 2002; Paton 2002; Schuster 1974.

Habitat. On shaded, damp, decaying logs. Elevation from 25 to 170 m.

Distribution. Cephalozia bicuspidata subsp. *lammersiana* occurs in Europe, Asia, and North America. Calif. Geographic Regions: **CR**: Tehama Co. *Showers 3846* (SFSU), **KR**: Del Norte Co. *Doyle 9771* (UC), **NC**: Humboldt Co. *Doyle 10588* (perianths) (UC).

Cephalozia connivens (Dicks.) Lindb.

Distinctive features. For this autoicous species look for a) leaves nearly horizontally inserted, long-decurrent on the dorsal stem surface, and with distinctly connivent lobe apices, b) stem dorsal epidermal cells 42–75 μm wide × 60–102 μm long, c) cells at the base of the leaf lobes 30–56 μm wide × 41–75 μm long or longer, d) apices of terminal cells of leaf lobes usually with additional wall thickening, e) absence of underleaves and stolons, and f) a perianth mouth that is deeply laciniately lobed with lobes ending in uniseriate filaments 2–6 cells long.

Separation. Both *C. connivens* and *C. lunulifolia* have nearly circular, conspicuously decurrent leaves with connivent lobes, and apices of terminal cells of leaf lobes with additional wall thickening. *Cephalozia connivens* can be separated by a) the larger size of the stem dorsal epidermal cells 42–75 μm wide (vs. stem dorsal epidermal cells 24–50 μm wide in *C. lunulifolia*), b) cells larger at the base of leaf lobes 30–56 μm wide and 41–75 μm long (vs. cells at the leaf lobe base 20–35 μm and 25–42 μm), and c) perianth mouth laciniately lobed, with lobes ending in 2–6 uniseriate cells (vs. perianth mouth crenulate/dentate, with 1-celled teeth).

Illustrations. Damsholt 2002; Paton 1999; Schuster 1974.

Habitat. On shaded, damp decaying logs and wet humus. Elevation from 136 to 1500 m.

Distribution. Cephalozia connivens occurs in Europe, Asia, and North America. Calif. Geographic Regions: **KR**: Trinity Co. *Doyle 8658* (UC).

Cephalozia lunulifolia (Dumort.) Dumort.

Distinctive features. This autoicous/dioicous species is highly variable, depending on whether growing in wet or dry habitats, or on mineral soil or decaying wood. Look for a) semi-circular leaves nearly horizontally to obliquely inserted, clearly long-decurrent and with connivent lobe apices, b) stem dorsal epidermal cells 24–50 μm wide × 45–60 μm long, c) cells at the base of the leaf lobes 20–35 μm wide × 26–42 μm long, d) apices of terminal cells of leaf lobes usually with thickened walls, e) absence of underleaves and stolons, and f) a perianth mouth that is crenate/dentate, usually with 1-celled elongate teeth.

Separation. Cephalozia lunulifolia can be confused with *C. connivens* and some growth forms of *C. pleniceps*. See *C. connivens* for separation from that species. *Cephalozia lunulifolia* is separated from *C. pleniceps* by a) leaves distinctly long-decurrent (vs. leaves little or not decurrent in *C. pleniceps*), b) leaf lobe apices clearly connivent (vs. leaf lobe apices little or not connivent), c) apices of terminal cells of leaf lobes usually with additional wall thickening (vs. apices of terminal cells usually without additional wall thickening), and d) smaller cells at the leaf lobe base 20–35 μm wide × 26–42 μm long (vs. cells at the leaf lobe base 20–60 μm wide × 24–65 μm long).

Illustrations. Damsholt 2002; Paton 1999; Schuster 1974.

Habitat. Shaded, moist surfaces; commonly on decaying logs and stumps, but also on humus, mineral soil and rocks; Elevation from 50 to 435 m.

Distribution. Cephalozia lunulifolia occurs in Europe, Asia, and North America. Calif. Geographic Regions: **CC**: Monterey Co. *Doyle 8172* (UC), **KR**: Trinity Co. *Doyle 8655* (UC), **NC**: Mendocino Co. *Doyle 10526* (UC), **SN**: Placer Co. *Doyle 9974* (UC).

Cephalozia pleniceps (Austin) Lindb.

Distinctive features. For this autoicous species look for a) leaves nearly semi-circular and usually strongly concave, obliquely inserted, and only slightly decurrent on the dorsal stem surface, b) leaf

lobes not or only little connivent, c) dorsal epidermal cells 40–60 μm wide, d) cells at the base of the leaf lobe 28–36 μm wide × 33–55 μm long, e) apices of terminal cells of leaf lobe apices usually without walls thickened more than the cell middle or base, f) stolons frequently present, g) underleaves usually absent, but occasionally small subulate underleaves or 2–3-celled slime-hairs present near the shoot apex, and h) perianth mouth crenulate to dentate.

Separation. See *C. lunulifolia* for separation from that species. *Cephalozia pleniceps* is separated from *C. connivens* by a) dorsal leaf margin not or only little decurrent (vs. dorsal leaf margin long-decurrent in *C. connivens*), b) smaller cells at the lobe base, mostly 20–60 μm wide × 24–54 μm long (vs. cells at the leaf lobe base 30–56 μm wide × 45–75 μm long), c) apices of terminal cells of leaf lobes usually without additional wall thickening (vs. apices of terminal cells usually with additional wall thickening), and d) perianth mouth crenulate to dentate (vs. perianth mouth laciniately lobed ending in 2–5 uniseriate cells).

Illustrations. Damsholt 2002; Howe 1899; Paton 1999; Schuster 1974.

Habitat. Usually on damp, peaty soil near margins of marshy and boggy areas; less often on shaded rocks and decaying logs. Elevation from 1424 to 3270 m.

Distribution. Cephalozia pleniceps occurs in Europe, Asia, and North America. Calif. Geographic Regions: **CR**: Shasta Co. *Doyle 9861* (perianths) (UC), **KR**: Siskiyou Co. *Doyle 9255* (UC), **MP**: Modoc Co. *Doyle 8643* (UC), **NC**: Sonoma Co. *Howell 670* (CAS), **SN**: Fresno Co. *Doyle 10215* (perianths) (UC).

Cephaloziella (Spruce) Schiffn. 1893
(Cephaloziellaceae)

Plants of this genus are small, less than 0.5 mm wide × up to 1.2 cm long, and often threadlike. The study of these plants requires a steady hand, a compound microscope, and a high frustration threshold.

Mature, typical plants, upon which species descriptions are based, usually are readily identified. Unfortunately, non-typical plants are common and some vegetative plants cannot be identified with certainty. For example, plants collected during the early flush of growth following the onset of rain or snowmelt can look unlike plants collected later in the season from the same population. Under some environmental conditions, such as during prolonged rain and cloudy periods, species that normally are pigmented can lack pigmentation, and leaf shape, cell size and wall thickness can be "non-typical".

Things to look for include a) in the field, search thoroughly for reproductive plants, because details of reproduction can be helpful in identification, b) the presence or absence of underleaves, including whether underleaves occur only on reproductive, but not vegetative shoots, c) the number of oil-bodies in mid-leaf cells, d) the number of cells across the base of the leaf lobe, e) the width and length of cells at the base of leaf lobes, and f) whether the leaf margins are smooth or have short or long teeth.

Cephaloziella superficially can resemble small or etiolated plants of *Cephalozia*. *Cephaloziella*, however, a) lacks a large, nearly translucent stem epidermal cells (called a hyalodermis), b) has oil-bodies in leaf cells, and c) usually has 2-celled gemmae, whereas *Cephalozia* has a hyalodermis, lacks oil-bodies in leaf cells, and has only 1-celled gemmae.

Six species plus one variety in California.

Species Key

1. Underleaves absent on vegetative regions of stems. . . . . **2.**
1. Underleaves common or infrequent on some or all vegetative regions of stems. . . . . **3.**
2. Leaf margins spinose-dentate; gemmae angular; no underleaves on reproductive stems. . . . . **C. turneri**
2. Leaf margins not spinose-dentate; gemmae ovoid; underleaves present on reproductive stems. (some shoots of *C. rubella var. sullivantii* and *C. spinigera* also might key here) . . . . **C. hampeana**
3. Underleaves infrequently developed on vegetative stems. . . . . **4.**
3. Underleaves always present on vegetative stems. . . . . **5.**
4. Leaves deeply bilobed, more than 0.8 their length; cells at base of lobes mostly 14–22 μm long; leaf base occasionally with 1 or 2 marginal teeth. . . . . **C. spinigera**
4. Leaves bilobed less than 0.6 their length; cells at base of lobes 12–25 μm long; leaf base without marginal teeth. . . . . **C. rubella var. sullivantii**

5. Leaf margins smooth; leaf cells with thin or moderately thickened walls; cells at lobe base large, 12–20 µm wide; paroicous. . . . . **C. stellulifera**
5. Leaves margins smooth to dentate; leaf cells with thickened walls; cells at lobe base small, 9–15 µm wide; dioicous. . . . . **6.**
6. Plants green to reddish to blackish; leaf lobe margins smooth; abaxial leaf surface smooth; gemmae reddish, 2-celled. . . . . **C. divaricata var. divaricata**
6. Plants green to gray-green to greenish-brown; leaf lobe margins dentate; abaxial leaf surface with coarse, conical protuberances; gemmae greenish, usually 1-celled. **C. divaricata var. scabra**

Cephaloziella divaricata (Sm.) Schiffn

Plants of this dioicous species grow in loose to compact mats or as individual shoots among bryophytes. Female and male plants often grow in close proximity; in the field, look for female plants with perianths and then search for nearby male plants. Male plants have spike-like clusters of overlapping bracts, each with a concave base subtending one antheridium. For species identification, look for a) underleaves consistently present on vegetative shoots, b) leaf lobes 6–9 cells wide at the base, c) cells at the leaf lobe base 9–15 µm wide, and d) distinctive white perianth apices that contrast strongly with the perianth base and leafy shoots. **Note:** Gemmae develop on leaf margins, and gemmae-bearing leaves often are strongly erose and can appear "abnormal" in size and shape.

This species grows in a wide variety of habitats and exhibits great morphological diversity. Two varieties are recognized in California, var. *divaricata* and var. *scabra*. Gradations between the two varieties do exist. However, populations of var. *scabra* can be so strikingly different from those of var. *divaricata* that this publication follows the traditional approach in recognition of both as varieties.

The following combination of characteristics separates both varieties of *Cephaloziella divaricata* from other California species of *Cephaloziella*: a) underleaves consistently present on vegetative stems, b) leaf cells usually with thickened walls, c) leaf lobes 6–9 cells wide at the base, d) cells at base of leaf lobes 9–15 µm wide, and e) being dioicous.

Cephaloziella divaricata (Sm.) Schiffn. var. **divaricata**

Distinctive features. This is the most widespread and morphologically variable of the two varieties. The color varies from green to dark green (usually in more shaded and humid or wet habitats) to purplish or black (in exposed and summer-dry habitats). The shoot apex of new growth often has a reddish coloration, especially early in the growing season. Also look for a) leaf margins with no or few marginal teeth and b) the lack of cellular protuberances on the abaxial surface of the leaf.

Separation. Cephaloziella divaricata var. *divaricata* can be separated from var. *scabra* by a) usually entire leaf margins (vs. usually dentate leaf margins in var. *scabra*) and b) prominent cellular protuberances absent on the abaxial leaf surface (vs. prominent cellular protuberances present on the abaxial leaf surface).

Illustrations. Damsholt 2002; Paton 1999; Schuster 1980; Smith 1990.

Habitat. On soil, organic matter, rocks, surface of rocks and boulders. Elevation from 106 to 1067 m.

Distribution. Cephaloziella divaricata var. *divaricata* occurs in Europe, North Africa, North and South America, and New Zealand. Calif. Geographic Regions: **CC**: San Francisco Co. *Bourell 4392* (CAS), **KR**: Trinity Co. *Norris 72829* (UC), **NC**: Lake Co. *Shevock 17106* (CAS), **SC**: Los Angeles Co. *Sagar 259* (SFV), **SN**: Plumas Co. *Janeway 5391* (CHSC).

Cephaloziella divaricata (Sm.) Schiffn. var. **scabra** M. Howe

Distinctive features. This variety usually has a distinctive grayish-green or yellowish-green coloration. Examine mature, well-developed regions of the shoot. The apical regions of shoots developed early in the growing season, or of etiolated or weak shoots, can lack or have poorly developed leaf marginal teeth and abaxial protuberances. Use shoots from different parts of your collection for examination and look for a) leaves with dentate margins and b) prominent cellular protuberances on the abaxial leaf surfaces.

Separation. See *C. divaricata* var. *divaricata* for separation of these two varieties.

Illustrations. Frye and Clark 1945 (as *Cephaloziella papillosa* (Douin) Schiffn.)

Habitat. Mostly on shaded mineral soil, rock outcrops and cliff faces; less commonly on decaying wood. Elevation from 330 to 1100 m.

Distribution. *Cephaloziella divaricata* var. *scabra* occurs in North America. Calif. Geographic Regions: **CC**: Monterey Co. *Doyle 6526* (UC), **KR**: Del Norte Co. *Doyle 11027* (UC), **NC**: Mendocino Co. *Doyle 9079* (UC), **SN**: Calaveras Co. *Shevock 21740* (CAS).

Cephaloziella hampeana (Nees) Schiffn.

Distinctive features. This autoicous species of green to brownish-green plants a) lacks underleaves on vegetative stems regions, b) has thin-walled leaf cells, c) has leaf lobes usually with 6–12 cells at the base, these cells mostly 11–16 µm wide, and d) has 2–7 oil-bodies in median leaf cells.

Separation. *Cephaloziella hampeana* lacks underleaves on vegetative stem regions; in this, it resembles some stems of *C. rubella* var. *sullivantii*. *C. hampeana* can be separated by a) green to brownish-green shoots (vs. green to reddish or reddish brown shoots in *C. rubella* var. *sullivantii*), b) leaves with thin-walled cells (vs. leaves usually with thick-walled cells), c) leaf lobes bases mostly 6–12 cells wide (vs. leaf lobe bases mostly 3–5 cells wide), and d) 2–7 oil-bodies in median leaf cells (vs. 6–11 oil-bodies in median leaf cells).

Illustrations. Damsholt 2002; Paton 1999; Schuster 1980; Smith 1990.

Habitat. Soil.

Distribution. *Cephaloziella hampeana* occurs in Europe, Asia, and North America. Calif. Geographic Regions: **SC**: Los Angeles Co. *Kingman 704* (YU) (Reported by Hong 1986; the specimen was not available for examination).

Cephaloziella rubella (Nees) Warnst. var. **sullivantii** (Austin) Müll. Frib.

Distinctive features. Like the other species of *Cephaloziella*, *C. rubella* is a highly variable plant with several named varieties; the variety *sullivantii* occurs in California. It has small and often inconspicuous underleaves on some, but seldom on all non-reproductive stem regions. Look for a) shoots usually with reddish-brown pigmentation, b) leaves bifid 0.5–0.75 their length and 3–5 cells wide at the lobe base, c) thick-walled cells at the lobe base mostly 9–14 µm wide, d) small underleaves sometimes present on vegetative stem regions, and e) 6–11 oil-bodies in median leaf cells.

Separation. *Cephaloziella rubella* can have infrequent to no underleaves on vegetative regions of the stem and can be confused with *C. hampeana*. See *C. hampeana* for separation from that species.

Illustrations. Damsholt 2002; Paton 1999; Schuster 1980; Smith 1990.

Habitat. On soil and decaying logs. Elevation mostly below 500 m.

Distribution. *Cephaloziella rubella* var. *sullivantii* occurs in Europe, Asia, and North America. Calif. Geographic Regions: **SN**: Ventura Co. *Haynes 2041* (YU) (Reported by Evans 1923 and Hong 1986; the specimen was not available for examination).

Cephaloziella spinigera (Lindb.) Jörg.

Distinctive features. This autoicous plant can be overlooked because it often grows as scattered shoots among other bryophytes. Shoots are light green in wet, shaded habitats and often copper-red in sunny locations. Look for a) leaves deeply divided to 0.9 their length into 2 narrow lobes, 2–5 cells wide at the lobe base, b) slightly elongate, evenly thick-walled cells at leaf lobe bases mostly 9–12 µm wide and 14–23 µm long, c) leaves occasionally with a small spinose tooth near the base of one or both lateral margins, d) cuticle of leaf weakly to coarsely papillose, and e) small subulate or bilobed underleaves often sparsely developed or lacking on some vegetative stem regions.

Separation. With the combination of a) slightly elongate cells at leaf bases, b) leaves often with marginal teeth, and c) sparse development of small underleaves, this species is not easily confused with other California species of *Cephaloziella*.

Illustrations. Damsholt 2002; Paton 1999; Schuster 1980; Smith 1990.

Habitat. On soil, often as scattered shoots in other bryophytes.

Distribution. *Cephaloziella spinigera* occurs in Europe, Asia, and North America. Calif. Geographic Regions: **MP**: Modoc Co. *Doyle 9652* (UC), **NC**: Mendocino Co. *Doyle 10513* (UC).

Cephaloziella stellulifera (Taylor) Schiffn.

Distinctive features. Shoots of this paroicous species usually are green to yellowish-green, and often have brownish wall pigmentation when growing in exposed habitats. Look for a) underleaves present on all vegetative stems, the underleaves mostly subulate, but occasionally lanceolate or bifid, b) leaves with narrow lobes mostly 4–7 cells wide at the lobe base, c) cells at the leaf lobe base thin- to slightly thick-walled, mostly 12–20 μm wide and 16–21 μm long, d) dorsal cortical cells mostly 12–14 × 18–35 μm, e) usually 2–8 oil-bodies per cell, and f) perianth mouth with elongate thick-walled cells.

Separation. Both *C. stellulifera* and *C. divaricata* consistently have distinct underleaves on vegetative stems. *C. stellulifera* is separated by a) paroicous sexual reproduction (vs. dioicous sexual reproduction in *C. divaricata*), b) brownish secondary wall pigmentation (vs. a reddish or purplish or blackish wall pigmentation), c) leaf cells thin to slightly thick-walled (vs. leaf cells moderately to strongly thick-walled), and d) cells at the leaf lobe base mostly 12–20 μm wide (vs. cells at the leaf lobe base 9–15 μm wide).

Illustrations. Damsholt 2002; Paton 1999; Schuster 1980; Smith 1990.

Habitat. On shaded soil. Elevation from 30 to 1700 m.

Distribution. *Cephaloziella stellulifera* occurs in Europe, Asia, and North America. Calif. Geographic Regions: **CC**: Santa Cruz Co. *Doyle 8855* (UC), **KR**: Shasta Co. *Doyle 9123* (UC), **SC**: Santa Barbara Co. *Shevock 20894* (CAS), **SN**: Tulare Co. *Shevock 17037* (CAS).

Cephaloziella turneri (Hook.) Müll. Frib.

Distinctive features. This distinctive, autoicous species usually grows in green, brown or reddish-brown patches. Look for a) leaves divided 0.65 or more their length, with margins conspicuously dentate to serrate, b) underleaves lacking on both vegetative and reproductive stems, c) polyangular gemmae, and d) plicate perianths.

Separation. With its deeply divided leaves with dentate to serrate margins and complete absence of underleaves, mature shoots of this species are not likely to be confused with other California species of *Cephaloziella*. Poorly developed plants (etiolated, young or from wet, dimly-light habitats) of *C. turneri* can be separated from *C. divaricata* var. *scabra* by the absence of underleaves (vs. underleaves present in *C. divaricata* var. *scabra*).

Illustrations. Damsholt 2002; Paton 1999; Schuster 1980; Smith 1990.

Habitat. Summer-dry habitats; exposed to partially shaded soil; occasionally on organic material and charred surface of stumps. Elevation from 120 to 1560 m.

Distribution. *Cephaloziella turneri* occurs in Europe, North Africa, and western North America. Calif. Geographic Regions: **CC**: San Benito Co. *Doyle 11257* (UC), **KR**: Del Norte Co. *Doyle 10630* (UC), **NC**: Humboldt Co. *Doyle 10065* (UC), **SC**: Los Angeles Co. *Sagar 361* (SFV), **SN**: Placer Co. *Doyle 8475* (UC).

Chiloscyphus Corda 1829
(Geocalycaceae)

These leafy liverworts generally occur in humid, damp and wet habitats. Leaves are succubous with smooth lateral margins. Leaf apices are rounded, truncate or emarginate.The leaf is decurrent on the dorsal stem surface. The conspicuous underleaves are bilobed and usually have a tooth on one or both sides. Rhizoids develop in tufts from the bases of underleaves.

The genus *Lophocolea* can be confused with *Chiloscyphus* and some bryologists (e.g., Damsholt, 2002) treat species of *Lophocolea* as species of *Chiloscyphus*. The two are treated as separate genera in this publication. *Chiloscyphus* can be separated by a) leaf apices truncate, rounded or emarginate, (vs. apices of some to all leaves shallowly to deeply bilobed in *Lophocolea*), and b) perianths at the apices of short lateral branches that have reduced leaves (vs. perianths at the apices of main branches that have normal leaves). See also Grolle (1995) for reasons to maintain *Lophocolea* and *Chiloscyphus* as separate genera.

Two species in California.

SPECIES KEY

1. Median leaf cells generally 17–33 (seldom to 35) μm wide × 23–45 μm long (seldom longer); oil-bodies usually 2–4 per median leaf cell; perianth mouth lobes entire or with short teeth. . . . . **C. polyanthos**
1. Median leaf cells generally 25–45 *u*m wide × 33–64 *u*m long (or longer); oil-bodies usually 4–8 (or more) per median leaf cell; perianth mouth lobes clearly toothed to spinose. . . . . **C. pallescens**

The two California species are polymorphic and occasionally difficult to separate. The two species can confidently be separated on the basis of differing chromosome numbers, *C. polyanthos* has 9 chromosomes and *C. pallescens* has 18, but this information is not helpful for the identification of dried specimens. Although shoot coloration, and median and marginal leaf cell size varies considerably within each species, cells of *C. pallescens* mostly are larger than those of *C. polyanthos*. We have not found that the width of marginal cells at the leaf apices was any more reliable in separating these two species than the use of mid-leaf cell width and length. Make all measurements on leaves from fully mature regions of the shoot, and make measurements on leaves from several shoots. Details of the perianth mouth also can be used to separate the two species; unfortunately, most collections consist only of vegetative plants. Whenever possible, therefore, examine fresh plants to determine the number of oil-bodies in median cells of mature leaves and keep these data with the specimen.

Chiloscyphus pallescens (Ehrh. ex Hoffm.) Dumort.

Distinctive features. Shoots generally are pale-, yellowish- to whitish-green, to a dark green. Look for a) oil-bodies usually 4–8 (or more) in each mature median leaf cell, b) median leaf cells mostly 25–45 μm wide × 33–64 μm long (or longer), c) leaves usually only slightly decurrent on the dorsal stem surface and often with truncate apices, and d) perianth mouth distinctly toothed to ciliate.

Separation. The two species of this genus exhibit great and overlapping variation in color, habitat occurrence and median leaf cell size. The number of oil-bodies in mature median leaf cells of fresh plants is the easiest character to use: *C. pallescens* generally has 4–8 oil-bodies per cell; *C. polyanthos* generally has 2–4 oil-bodies per cell. In addition, *C. pallescens* has a) leaves slightly decurrent on the stem dorsal surface (vs. leaves clearly decurrent on the stem dorsal surface in *C. polyanthos*), and b) median leaf cells mostly 25–45 μm wide × 33–64 μm long (vs. median leaf cells mostly 17–33 μm wide × 23–45 μm long).

Illustrations. Damsholt 2002; Paton 1999; Schuster 1969; Smith 1990.

Habitat. On shaded soil, rocks and decaying logs; submerged, seasonally inundated or high humidity habitats. Elevation from 970 to 2356 m.

Distribution. Chiloscyphus pallescens occurs in Europe, Asia, and North America. Calif. Geographic Regions: **KR**: Del Norte Co. *Doyle 1968* (UC), **SN**: El Dorado Co. *Doyle 11167* (UC).

Chiloscyphus polyanthos (L.) Corda

Distinctive features. Shoots generally are a dull-, deep- to brownish-green; however, some populations are lighter green in color. Look for a) 2–4 oil-bodies in each mature median leaf cell, b) median leaf cells mostly 17–33 μm wide (seldom wider) × 23–45 μm long (seldom longer), c) leaves usually clearly decurrent on the dorsal stem surface and often with rounded, truncate or slightly emarginate apices, and d) perianth smooth or with short teeth.

Separation. See *C. pallescens* for separation.

Illustrations. Damsholt 2002; Paton 1999; Schofield 2002; Schuster 1969; Smith 1990.

Habitat. On shaded rocks, soil, organic debris, and decaying logs; usually seasonally inundated or permanently submerged; also above the water line. Elevation from 34 to 3030 m.

Distribution. Chiloscyphus polyanthos occurs in Europe, Asia, Africa, and North America. Calif. Geographic Regions: **CC**: San Mateo Co. *Doyle 8958* (UC), **CR**: Shasta Co. *Doyle 10165* (UC), **KR**:

Trinity Co. *Doyle 9793* (UC), **MP**: Modoc Co. *Doyle 9673* (UC), **NC**: Mendocino Co. *Doyle 10530* (UC), **SN**: Butte Co. *Doyle 11412* (UC).

Diplophyllum (Dumort.) Dumort. 1835
(Scapaniaceae)

Plants of this genus have complicate-bilobed leaves with the dorsal lobe smaller than the ventral lobe. Features of the genus include a) lingulate ventral lobes with rounded, obtuse or truncate apices, b) marginal cells of leaf lobes 15 μm wide or less, c) angular to stellate gemmae, and d) perianths that are slightly flattened and narrowed from above the middle to the mouth. *Douinia* and *Scapania* also have complicate-bilobed leaves with the dorsal lobe smaller than the ventral. Unlike *Diplophyllum*, *Douinia* has lanceolate leaf lobes that taper from near the base to an acute apex, and *Scapania* has a) ovoid to ellipsoidal gemmae, b) ventral leaf lobes that rarely are lingulate, and c) perianths that are not or only little narrowed to the mouth.

Three species in California.

Species Key

1. Ventral leaf lobe strongly decurrent; cells in middle of ventral lobe more than 20 μm wide, with prominent, rounded, knob-like (nodose) trigones; gemmae 2–4-celled, cubic often with rounded edges; perianths plicate from near the mouth to the base. . . . . **D. plicatum**
1. Ventral leaf lobe not decurrent; cells in middle of ventral lobe less than 20 μm wide and equally thick-walled (no trigones); gemmae usually 1-celled, stellate to bluntly stellate; perianths plicate above, but smooth toward the base. . . . . **2.**
2. Shoots small, less than 1.2 cm long; oil-bodies smooth in profile; gemmae not common; paroicous; perianth basal areas often with reddish coloration; mostly on soil; lower elevations toward the coast. . . . . **D. obtusifolium**
2. Shoots large, 1–3 cm long; oil-bodies coarsely papillose in profile; gemmae common; dioicous; perianths without reddish coloration; mostly on rocks; higher elevations. . . . . **D. taxifolium**

Diplophyllum obtusifolium (Hook.) Dumort.

Distinctive features. These paroicous plants usually grow in small pale- to yellowish-green patches, with shoots up to 1.2 cm long. Shoots are pale- to yellowish-green; in sunny exposures, the stem, leaf base and perianth base often develop vinaceous coloration. Look for a) rhizoids developing nearly to the stem apex, b) dorsal and ventral lobes with rounded apices, c) perianths frequently present, and d) antheridial bracts conspicuous, saccate, immediately below the perianth.

Separation. With shoots less than 1.2 cm long, rhizoids nearly to the stem apex, and perianths with a reddish basal coloration, this species should not be confused with *D. plicatum* or *D. taxifolium*.

Illustrations. Damsholt 2002; Paton 1999; Schuster 1974.

Habitat. On soil of banks, paths, crevices in rocks and cliff faces; rarely on decayed logs. Elevation from 50 to 500 m

Distribution. Diplophyllum obtusifolium occurs in Europe, Asia, and western North America. Calif. Geographic Regions: **KR**: Del Norte Co. *Doyle 10587* (UC), **NC**: Humboldt Co. *Doyle 1383* (UC).

Diplophyllum plicatum Lindb.

This is a rare species in Oregon; in California it is known from a single collection—intermixed with *Plagiochila porelloides* on a *Sequoia* trunk, Howland Summit area of Jedediah Smith Redwoods State Park, Del Norte County. On casual observation, it is about the same color and size as *P. porelloides* and was not noticed in the field. Examine field populations of *P. porelloides* carefully.

Distinctive features. These are large green to dark-green plants. Distinctive characteristics include: a) leaf lobes 2–4 times as long as wide, b) median cells of mature ventral lobes greater than 20 μm wide, with prominent nodose trigones, c) ventral lobes with decurrent bases and strongly toothed basal margins, and d) the cell walls of the ventral lobe teeth and adjacent leaf cells usually orange to orange-red. Reproductive plants have not been located in California.

Separation. This species is separated from other species in the genus by a) the median cells of the ventral lobe greater than 20 μm wide and with nodose trigones, and b) ventral lobes strongly decurrent and with orange-red toothed basal margins.

Illustrations. Frye and Clark 1946.

Habitat. Areas of high humidity and cool summer temperatures; on trunk of trees, intermixed with other liverworts. Elevation about 85 m.

Distribution. Diplophyllum plicatum occurs in the North Pacific, from NE Asia to coastal Alaska, then south to northern Oregon and disjunct to California. Calif. Geographic Regions: **KR**: Del Norte Co. *Doyle 7729* (UC).

Diplophyllum taxifolium (Wahlenb.) Dumort.

Distinctive features. These dioicous plants usually occur in large populations with shoots often more than 2.5 cm in length. Look for a) shoots that are green to grayish-green, occasionally yellowish-brown, b) median cells of the ventral lobe equally thick-walled, less than 20 μm wide, without trigones, c) dorsal lobe apices usually obtuse, and d) ventral leaf lobes non-decurrent, without teeth on the dorsal lobe margin. Populations with perianths are infrequent in California.

Separation. This species generally grows at higher elevations and more inland than does *D. obtusifolium*. It is separated from *D. obtusifolium* by a) shoots up to 2.5 cm long (vs. shoots less than 1.2 cm long in *D. obtusifolium*), b) shoots and perianths without reddish coloration, even in sun-forms (vs. shoots and perianths reddish in sun-forms, c) dorsal leaf lobes with obtuse apices (vs. dorsal leaf lobes with rounded apices), and d) being dioicous with infrequent sporophytes (vs. being paroicous and commonly with sporophytes). The absence of an orange-red, toothed and long decurrent basal margin of the ventral lobe separates *D. taxifolium* from *D. plicatum*.

Illustrations. Damsholt 2002; Paton 1999; and Schuster 1974.

Habitat. On sunny to shaded soil in crevices of rock outcrops, rock faces, deep canyons, and underhang of boulders in open talus slopes. Elevation from 1300 to 2150 m.

Distribution. Diplophyllum taxifolium occurs in Europe, Asia, and North America. Calif. Geographic Regions: **KR**: Trinity Co. *Norris 85408* (perianths) (UC), **NC**: Humboldt Co. *Norris 13344* (UC).

Douinia (C. E. O. Jensen) H. Buch 1928
(Scapaniaceae)

This genus has complicate-bilobed leaves with the dorsal lobe smaller than the ventral lobe. Look for a) dorsal and ventral leaf lobes lanceolate, tapering from near the base to the apex and b) irregular "waxy" markings on the surface of leaves. *Diplophyllum* and *Scapania* also have complicate-bilobed leaves with the dorsal lobe smaller than the ventral lobe. Unlike *Douinia*, *Diplophyllum* has a) ventral lobes lingulate with rounded or obtuse apices and b) lacks irregular "waxy" layers, and *Scapania* lacks a) perianth mouths with curved, branched cilia and b) irregular, "waxy" layers.
A monotypic genus.

Douinia ovata (Dicks.) H. Buch

Distinctive features. These dioicous plants are relatively small, less than 1.5 cm. long, and usually grow in glaucous green to yellowish-brown patches. Look for a) dorsal leaf lobes somewhat erect with apices pointed toward the stem apex, b) ventral leaf lobes flat with apices pointed outwards, b) dorsal and ventral lobes both tapering to an acute apex, c) trigones absent or small on the somewhat thickened walls of the median cells of the ventral lobe d) cell walls covered by irregular "waxy" material, and e) perianth mouths that have curved branched cilia and usually become whitish with age. Gemmae are absent.

Separation. This species can be confused with *Anastrophyllum minutum*. *Douinia* can be separated by a) the leaf surface with irregular "waxy" material (vs. the leaf surface without "waxy" material in *A. minutum*), b) gemmae absent (vs. gemmae frequently present), and c) perianth mouth with curved, branched teeth (vs. perianth mouth with unbranched cilia in *A. minutum*).

Illustrations. Damsholt 2002; Frye and Clark 1946; Paton 1999; Schofield 2002; Smith 1990.

Habitat. In canyons; on and around rocks; near sea-level to 1500 m.

Distribution. Douinia ovata occurs in Europe and western North America. Calif. Geographic Regions: **KR**: Siskiyou Co. *Wheeler 8292* (UC), **NC**: Humboldt Co. *Norris 23487* (perianths) (ABSH).

Frullania Raddi 1818
(Frullaniaceae)

Select for study only leaves and underleaves from healthy, mature shoots and main branches. Observations on immature, diseased or etiolated plant parts can result in incorrect identification.

This genus has complicate-bilobed leaves with incubous dorsal lobes that are larger than the ventral lobes. Distinctive features are a) leaves bilobed nearly to the base, b) ventral lobes (often called lobules: technically, a lobule is the smaller of the two lobes in complicate-bilobed leaves of *Frullania, Porella, Radula, Diplophyllum*, *Douinia*, and *Scapania*; its use often is incorrectly restricted to the ventral lobes only of *Frullania*) somewhat flattened (explanate) or form distinctive helmet-shaped (galeate) or cylindrical structures, c) dorsal lobes of several species with scattered, groups or rows of specialized colored cells (= ocelli), d) bilobed underleaves, e) rhizoids develop in tufts from the base of the underleaves, and f) perianths constricted to a beak-like mouth. The genus has both paroicous and dioicous species. For diocous species search populations carefully for perianths, which indicate nearby male plants.

Frullania, Porella and *Radula* have complicate-bilobed leaves with incubous dorsal lobes that are larger than the ventral lobes. However, a) the underleaves of *Porella* are entire (vs. underleaves bilobed in *Frullania*), and b) *Radula* lacks underleaves (vs. underleaves present).

Five species in California. The Evans (1897) monograph of North American species of *Frullania* contains excellent keys, descriptions and illustrations of all five California species.

Species Key

1. Ventral lobes helmut-shaped (galeate) about as long as wide, or frequently flattened (explanate); perianth terminal on the main stem or a long branch. . . . . **2.**
1. Ventral lobes cylindrical, clearly longer than wide; perianth terminal on a short lateral branch. . . . . **3.**
2. Erect branches with caducous leaves present in mature parts of healthy populations; leafy stems 0.5–0.7 mm wide; ventral lobes usually galeate; dioicous. . . . . **F. bolanderi**
2. Erect branches with caducous leaves absent; leafy stems 0.8–1.2 mm wide; ventral lobes mostly explanate; autoicous. . . . . **F. catalinae**
3. Dorsal lobes on main branches usually with a single or double median line of discolored cells (ocelli); underleaves gradually narrowed to the base; lobes each usually with a broad shoulder near the middle. . . . . **F. franciscana**
3. Dorsal lobes on main branches usually without discolored cells, but when present, seldom in a single line; underleaves auriculate or narrowed to the base; lobes mostly without a broad shoulder near the middle. . . . . **4.**
4. Underleaves usually clearly auriculate at the base; ventral lobe separated from the stem by more than half the ventral lobe width; perianths gradually narrowed from about the middle to near the beak. . . . . **F. nisquallensis**
4. Underleaves either gradually narrowed to the base or auriculate; ventral lobe separated from the stem by less than half the ventral lobe width; perianths truncate, abruptly contracted from near the apex to the beak. . . . . **F. californica**

Excluded. Frullania inflata Gottsche. Clark and Svihla (1944) placed *F. catalinae* A. Evans in synonymy with *F. inflata*. Subsequently, some California specimens of *F. catalinae* were annotated, and other collections identified, as *F. inflata*. This synonymy was not accepted by Stotler and Crandall-Stotler (1977) and Hong (1989). Specimens examined during the present study support the conclusion that *F. catalinae* and *F. inflata* are separate species. All California specimens labelled *F. inflata* examined in this study, including those cited by Frye and Clark (1946) and Hong (1989), are confirmed as *F. catalinae*. *Frullania inflata* could not be confirmed for California.

Frullania bolanderi Austin

Distinctive features. These green to reddish-brown plants are 0.5–0.7 mm wide and usually tightly adherent to the substrate. The most distinctive feature, visible with a 10x handlens, is the presence in most populations of short, abruptly erect branches with leaves that detach (caducous) as propagules in asexual reproduction; modified underleaves remain on the erect branches. Also look for a) ventral lobes mostly galeate with a wide mouth, but occasionally flat (explanate), b) underleaves bifid to about 0.5 their length and margins usually with one or two blunt teeth, and c) perianths abruptly contracted near the apex to a short, broad beak.

Separation. The presence of short, stiffly erect branches with caducous leaves separates *F. bolanderi* from other California species. When erect branches with caducous leaves are absent (e.g., from small populations), the small shoot width of 0.5–0.7 mm wide coupled with mostly galeate ventral lobes separates this species from others in the genus.

Illustrations. Damsholt 2002; Evans 1897; Schuster 1992a.

Habitat. On bark of angiosperms; less commonly on trunks of young conifers; occasionally on rocks, soil and decaying wood. Elevation from near sea-level to 2000 m, but mostly from 20 to 1500 m.

Distribution. Frullania bolanderi has the interesting distribution of eastern Asia, northeastern North America (Canada and New England), and western North America. Calif. Geographic Regions: **CC**: Alameda Co. *Shevock 26218* (CAS), **CR**: Tehama Co. *Doyle 8614* (UC), **KR**: Trinity Co. *Doyle 5914* (UC), **NC**: Lake Co. *Doyle 10005* (UC), **SC**: San Diego Co. *Stark 412* (MO), **SN**: Yuba Co. *Doyle 9594* (UC).

Frullania californica (Austin) A. Evans

Distinctive features. Plants of this dioicous species usually are green in shaded, humid habitats, and brownish-red in sunnier, drier habitats. Look for a) dorsal lobes without discolored cells, or, when present, few and scattered, and only rarely in a short median line, b) the dorsal lobe apex rounded, obtuse or acute, c) median cells of the dorsal lobes 10–20 μm wide, d) ventral lobes cylindrical and separated from the stem by less than 0.5 their width, e) underleaves bilobed about 0.5 their length or less, with lobe margins flat or sometimes slightly reflexed, f) underleaves gradually narrowed to the base or occasionally auriculate, and g) perianths truncate, abruptly contracted near the apex to a short beak.

Separation. This species can be separated from *F. franciscana* by a) the usual absence of a single or double median line of discolored cells in the dorsal lobe (vs. the usual presence of 1–2 rows of discolored cells in *F. franciscana*), and b) underleaves bilobed less than 0.5 their length (vs. underleaves bilobed 0.5 or more their length). Populations of *F. californica* that have dorsal lobes with a high proportion of acute to nearly acuminate apices, or underleaves with auriculate bases can be confused with *F. nisquallensis*. *Frullania californica* is separated by a) underleaf lobe margin and apex mostly not (or only slightly) reflexed (vs. underleaf lobe margin and apex strongly reflexed in *F. nisquallensis*), and b) perianths truncate, abruptly contracted to a short beak (vs. perianths more gradually narrowed to a beak).

Illustrations. Evans 1897; Clark and Frye 1928.

Habitat. Shaded, humid areas, usually near canyon bottoms; on bark, especially of angiosperms and young conifers; also on logs, rock outcrops and limestone boulders. Elevation between 15 and 1000 m, but mostly below 650 m.

Distribution. Frullania californica is endemic to western North America. Calif. Geographic Regions: **CC**: Contra Costa Co. *Shevock 24535* (UC), **KR**: Siskiyou Co. *Doyle 9281* (UC), **NC**: Sonoma Co. *Parks 2966* (CAS), **SC**: Santa Barbara Co. *Bratt s.n.* (9 November 1993) (UC).

Frullania catalinae A. Evans

Distinctive features. This is our only paroicous species of the genus. The plants often grow in large reddish-brown mats. Look for a) dorsal leaf lobes generally squarrose, with median cells 16–20 μm wide and 20–36 μm long, b) ventral lobes mostly explanate (but both explanate and galeate lobes can occur on the same stem), c) underleaves bifid to about 0.5 their length, the lobes often with a blunt

tooth or angulation on each lateral margin, d) perianths gradually narrowed from near the middle to a short apical beak (**caution:** a few perianths in some populations can be abruptly constricted near the apex.), and e) bracteoles connate on one margin with bracts.

Separation. Frullania catalinae is separated from *F. inflata* by a) perianths gradually narrowed from near the middle to a short apical beak (vs. perianths truncate, abruptly narrowed near the apex to a short beak in *F. inflata*), b) dorsal leaf lobes generally squarrose (vs. dorsal leaf lobes mostly flat), c) underleaves bifid to about 0.5 their length, the lobes on robust stems usually with blunt marginal teeth (vs. underleaves bifid to about 0.3 their length, the lobes without blunt marginal teeth); and d) bracteoles connate on one side with bracts (vs. bracteoles free on both sides from bracts). *Frullania catalinae is separated* from *F. bolanderi* by a) short, erect branches with caducous leaves absent (vs. branches with caducous leaves present in *F. bolanderi*), b) ventral lobes mostly explanate (vs. ventral lobes mostly galeate), and c) perianths gradually narrowed toward the apex (vs. perianths truncate, abruptly contracted at the apex.

Illustrations. Evans 1897.

Habitat. Shaded trunks of angiosperms and rock outcrops. Elevation from 15 to 405 m; mostly below 250 m.

Distribution. Frullania catalinae is endemic to coastal California. Calif. Geographic Regions: **CC**: San Luis Obispo Co. *Doyle 5752* (UC), **SC**: Los Angeles Co. *McClatchie 550* (Type!) (YU).

Frullania franciscana M. Howe

Distinctive features. Plants of this dioicous species can be green, yellow-green or reddish-brown. Distinctive features include a) dorsal leaf lobes mostly with 1–2 (occasionally 3) median lines (sometimes incomplete) of discolored cells (ocelli), b) dorsal lobes with rounded, obtuse or apiculate apices and usually with narrow and acute sinuses, c) ventral lobes cylindrical, separated from the stem by 0.5 or more of the lobe width, d) underleaves bilobed 0.5 their length or more, e) underleaf margin usually with a broad angulation about the middle of one or both lobes, f) underleaf gradually narrowed to the base (not auriculate), and g) perianth truncate, abruptly contracted from near the apex to the beak.

Separation. This species can be confused with *F. californica* and *F. nisquallensis*. It is separated from both *F. californica* and *F. nisquallensis* by a) the dorsal lobes usually with 1–2 (or three) median lines of discolored cells, and b) the underleaves gradually narrowed to the base (not auriculate).

Illustrations. Clark and Frye 1928; Evans 1897; Howe 1894.

Habitat. Shaded, humid habitats; usually on trunks and branches of angiosperms; occasionally on boulders. Elevation between 3 and 200 m; mostly below 110 m.

Distribution. Frullania franciscana is endemic to the Pacific Coast of North America. Calif. Geographic Regions: **CC**. San Mateo Co. *Whittemore 4067* (CAS), **KR**. Del Norte Co. *Doyle 10680* (UC), **NC**. Mendocino Co. *Doyle 10447* (UC).

Frullania nisquallensis Sull.

Distinctive features. Plants of this dioicous species vary from greenish to yellow-brown to reddish-brown. Look for a) dorsal lobe apices usually acute or acuminate, b) dorsal lobes with no (occasionally a few) scattered discolored cells, only rarely in a line, c) ventral lobes cylindrical, separated from the stem by about the lobe width, d) underleaf shallowly lobed, divided 0.25 to 0.3 their length, clearly auriculate at the base, and with or without short marginal basal spurs, e) underleaf lobe strongly reflexed on mature stems, and f) perianths mostly somewhat fusiform, gradually narrowing from about the middle to a beaked apex.

Separation. For separation from *F. californica* and *F. franciscana*, see comments under those species.

Illustrations. Evans 1897; Clark and Frye 1928; Schofield 2002.

Habitat. On angiosperms, gymnosperms, logs, and rocks. Elevation between 10 and 625 m.

Distribution. Frullania nisquallensis is endemic to western North America. Calif. Geographic Regions: **CC**: San Francisco Co. *Howe 198* (ABSH), **KR**: Del Norte Co. *Doyle 7723* (UC), **NC**: Humboldt Co. *Doyle 10580* (UC).

Geocalyx Nees 1836
(Geocalycaceae)

Plants of this yellowish- to grayish-green genus have a) rhizoids from the stem surface and underleaf base, b) leaf cells with distinct trigones, c) underleaves large and deeply divided, and d) a sporophyte that develops in a fleshy, rhizoid-covered, subterranean structure, called a marsupium.
One species in California.

Geocalyx graveolens (Schrad.) Nees

Distinctive features. These are opaque yellow- to olive-green plants with succubous leaves. They often grow in loose patches and are aromatic when living. Look for a) leaves shallowly bilobed with slightly unequal lobes, b) underleaves divided nearly to the base and appressed closely to the stem, c) underleaf lobes entire and often nearly parallel, d) rhizoids densely developed and often obscuring the underleaves except near the shoot apex, and e) lack of gemmae development.

Separation. With its a) opaque shoots, b) aroma of living plants, c) large and deeply bifid underleaves closely appressed to the stem and nearly obscured by dense rhizoid growth, and d) lack of gemmae, *G. graveolens* is not easily confused with other California liverworts.

Illustrations. Damsholt 2002; Frye and Clark 1945; Paton 1999; Schofield 2002; Schuster 1980; Smith 1990.

Habitat. Shaded, damp logs and organic matter; also on damp mineral soil; Elevation from 120 to 1135 m.

Distribution. Geocalyx graveolens occurs in Europe, Asia, and North America. Calif. Geographic Regions: **CC**: Santa Cruz Co. *Doyle 8915* (UC), **KR**: Siskiyou Co. *Doyle 9169* (UC), **NC**: Humboldt Co. *Norris 72078* (CAS), **CR** Tehama Co. *Doyle 4030* (UC).

Gymnocolea (Dumort.) Dumort. 1835
(Jungermanniaceae)

Species of this dioicous genus often occur in green to brownish to blackish mats. Look for a) leaves bilobed, obliquely inserted, succubous and widest about the middle, b) leaf cells with equally thickened-walls, c) rhizoids with scattered development on the stem, and d) perianths smooth (not plicate), contracted near the apex to a non-beaked mouth.
One species in California.

Gymnocolea inflata (Huds.) Dumort.

Distinctive features. This is a variable species. The shoots are green and lax in shaded and submerged habitats; shoots usually are in erect brownish-black patches, often with a somewhat burnt appearance in exposed habitats. A distinctive feature is the development of apically inflated perianths which, in the absence of fertilization, detach (caducous) and become a means of asexual reproduction. Thoroughly search field populations for these perianths. For vegetative plants, look for a) leaves generally widest about the middle, b) leaf lobes with obtuse to rounded apices and entire lateral margins, c) median leaf cells 17–29 μm wide × 20–42 μm long and marginal cells 15–33 μm wide, d) leaf cells with evenly thickened walls without trigones, e) underleaves scarce and vary in form from 1–3 celled papillae, to subulate to bilobed, and f) larger underleaves associated with branching frequently present.

Separation. With leaves wider about the leaf middle, rounded leaf lobes, caducous perianths, and sparse development of underleaves, *G. inflata* is easily separated from other California liverworts. In its color and lax growth in boggy habitats, it can be confused with *Cladopodiella fluitans*, a liverwort not yet found in California. *Cladopodiella fluitans*, however, has a) frequent development of distinct subulate or lanceolate underleaves, with 1-celled slime-filaments on the lateral margins (vs. sparse development of underleaves, without slime-filaments in *G. inflata*), b) larger median leaf cells, 28–44 μm wide and 32–45 μm long (vs. median leaf cells 17–29 μm wide and 20–42 μm long), and c) non-caducous perianths (vs. caducous perianths).

Illustrations. Damsholt 2002; Paton 1999; Schofield 2002; Schuster 1969; Smith 1990.

Habitat. Sunny to shaded sites subject to seasonal flooding, such as pond and lake margins, bogs, and seepages. Elevation mostly from 2250 to 3350 m, but around 160 m in *Sphagnum* bogs of Mendocino Co.

Distribution. Gymnocolea inflata occurs in Europe, Asia, and North America. Calif. Geographic Regions: **CR**: Shasta Co. *Doyle 10824* (UC), **MP**: Modoc Co. *Doyle 9671* (UC), **NC**: Mendocino Co. Kellman 2205 (CAS), **SN**: Mono Co. *Doyle 6814* (UC), **SNE**: Inyo Co. *Shevock 15338* (CAS).

Gymnomitrion Corda 1829
(Gymnomitraceae)

Gymnomitrion is a distinctive genus with a) erect shoots often in tightly appressed, compact tufts, b) bifid leaves closely over-lapping and appressed (like roof tiles) so that the stem is not visible, c) leaf margins usually with strongly thickened cell walls, and d) perianths lacking or vestigial.

Two species in California.

Species Key

1. Leaf lobe tips mostly acute; lobe margins entire to weakly crenulate toward the apex (but mostly smooth toward the base); lobe sinus usually open near the base. . . . . **G. concinnatum**
1. Leaf lobe tips mostly obtuse or rounded, occasionally apiculate; lobe margins crenulate from apex to base; sinus between lobes usually closed near base. . . . . **G. obtusum**

Gymnomitrion concinnatum (Lightf.) Corda

Distinctive features. Look for a) leaf lobe apices mostly acute ending in 1–2 superposed cells, b) lobe margins smooth or weakly crenulate near the apex, but smooth toward the base, and c) leaf lobe sinus acute and usually open.

Separation. Gymnomitrion concinnatum is morphologically variable and occasionally can be difficult to separate from *G. obtusum*. Look carefully at the leaf apices, sinuses and margins. In *G. concinnatum* a) the lobe apex mostly is acute (vs. lobe apex mostly is obtuse or rounded in *G. obtusum*, although some apices often are apiculate), b) lobe sinus open (vs. lobe sinus closed, the inner lobe margins touch or overlap near the lobe base), and c) the leaf margin near the lobe apex is entire or weakly crenulate (vs. leaf margin from the apex nearly to the leaf base is clearly crenulate).

Illustrations. Damsholt 2002; Frye and Clark 1943; Paton 1999; Schuster 1974; Smith 1990.

Habitat. Shaded, humid rock outcrops and surface of boulders; Elevation from 115 to 1800 m.

Distribution. Gymnomitrion concinnatum occurs in Europe, Asia, and North America. Calif. Geographic Regions: **KR**: Del Norte Co. *Norris 10881* (UC).

Gymnomitrion obtusum Lindb.

Distinctive features. Plants of this species often occur in compact, whitish tufts. Look for a) leaf lobe apex mostly obtuse or rounded (a few lobe apices often can be apiculate), b) lobe margins distinctly crenulate to the lobe base, and c) lobe sinuses acute to rounded, and usually closed (bases of the lobe inner margins touch or overlap) just above the sinus base.

Separation. Gymnomitrion obtusum and *G. concinnatum* share many features and occasionally are difficult to separate. See *G. concinnatum* for separation from that species.

Illustrations. Damsholt 2002; Frye and Clark 1943; Paton 1999; Schofield 2002; Schuster 1974; Smith 1990.

Habitat. Shaded boulder and cliff surfaces. Elevation above 1100 m.

Distribution. Gymnomitrion obtusum occurs in Europe and North America. Calif. Geographic Regions: **KR**: Del Norte Co. *Jessup 7406* (SOU), **SN**: El Dorado Co. *Norris 58397* (UC).

Gyrothyra M. Howe 1897
(Gyrothyraceae)

Distinctive features of this genus include a) large underleaves bifid with lanceolate lobes, b) leaf cells with conspicuous trigones, c) rhizoids developing near differentiated cushions on stem tissue, and d) capsules dehiscing by 4 long helical valves.
A monotypic genus.

Gyrothyra underwoodiana M. Howe

Distinctive features. The shoots of this species are sparingly branched and usually light green in color. Look for a) rhizoids mostly from around reddish multicellular cushions on the ventral stem surface (a few rhizoids often arising from cushion cells), the cushions are colorless near the stem apex and conspicuously reddish in older stem areas, b) thin-walled leaf cells with conspicuous triangular to bulging trigones, c) oil-bodies gray, ellipsoidal, 2–4 per median leaf cell, d) underleaves large, divided more than 0.5 their length into 2 lanceolate segments, the tips of which usually terminate with 2–4 uniseriate cells (underleaves are easier to see at the shoot apex because of the dense growth of rhizoids in older stem regions), and e) sporophyte capsules dehiscing by 4 long, narrow helical valves.

Separation. With the combination of a) succubous leaves with thin walls and triangular to bulging trigones, b) underleaves large and deeply bilobed, c) rhizoids surrounding reddish cushions on mature stem areas, and d) helical valves on the sporophyte capsule, *G. underwoodiana* should not be confused with other liverworts. The presence of large underleaves separate this plant from similar sized species of *Jungermannia* (a genus without underleaves).

Illustrations. Clark and Frye 1928; Howe 1897b; Howe 1899; Schofield 2002.

Habitat. On shaded, moist bare soil of hillsides, and road and trail banks. Elevation from 50 to 1200 m.

Distribution. Gyrothyra underwoodiana occurs only on the Pacific Coast of North America, where it occurs from Alaska to California. Calif. Geographic Regions: **KR**: Del Norte *Doyle 11049* (UC), **NC**: Marin Co. *Yurky 16* (NY 245632), **SN**: Butte *Doyle 11409* (UC).

Herbertus Gray 1821
(Herbertaceae)

This genus is questionable for California. Both ABSH and UC have packets labeled *Herbertus hutchinsiae* (=*Herbertus aduncus* (Dicks.) Gray subsp. *aduncus*) with the following information: Dodds, St. Lake; Pine Crest, Calif.; E. Morse; 1934. Pinecrest and Pinecrest Lake are east of Sonora on Calif. Highway 108, Stanislaus National Forest, Tuolumne, Co. No other collection of *Herbertus* is known for California. This species is abundant in British Columbia, rare in Washington, and known from only three localities in northern Oregon (Christy and Wagner 1996). In a note in the UC collection packet, Dan Norris wrote "This is surely a mis-statement of locality". The species name has been confirmed, but the State of collection likely is in error.

Herbertus aduncus (Dicks.) Gray subsp. **aduncus**

Distinctive features. Shoots usually are in large brownish-green to yellowish-brown mats. Look for a) lateral leaves and underleaves of similar size and shape, c) leaves bifid 0.75 or more their length, the lobes up to 6 times longer than wide, and d) a vitta of somewhat elongate cells extending 0.3 to 0.6 the lobe length. Slime papillae, when present, are unicellular (not stalked).

Separation. With its large shoots and strongly bifid leaves, *Herbertus* is more likely to be mistaken for a moss than a liverwort.

Illustrations. Damsholt 2002; Paton 1999; Schofield 2002; Schuster 1966; Smith 1990.

Habitat. No substrate was given. In the Pinecrest and Pinecrest Lake area, search for this plant on tree trunks, and shaded cliffs and boulders.

Distribution. Herbertus aduncus subsp. *aduncus* occurs in East Asia and northwestern North America. Calif. Geographic Regions: **SN?**: presence needs confirmation.

Jamesoniella (Spruce) F. Lees 1881
(Jungermanniaceae)

The Rick Dewey collection of *Jamesoniella autumnalis* (DC.) Steph., cited by A. Whittemore (in litt.), is not from California. This packet has no collection data or number. Dewey (personal communication) suggested that the plants came from a class at Humboldt State University; this possibility was confirmed by Dan Norris (personal communication). No herbarium specimen of *J. autumnalis* was located during the present study. This species could not be confirmed for California, but is retained in the key (see Damsholt (2002), Paton (1999), Schofield (2002), or Schuster (1969) for description and illustration).

Jungermannia L. 1753
(Jungermanniaceae)

Species of *Jungermannia* a) have succubous leaves that never are bilobed and seldom emarginate, b) lack underleaves, c) have rhizoids scattered on the stem, and on leaf bases in some species, d) lack gemmae in most species, and e) have cylindrical perianths that are smooth below, and plicate toward the mouth in most species. Perianths are at the stem apex or on a perigynium (a perigynium is a fleshy, tubular structure of stem origin that develops post-fertilization at the stem apex, surrounding the developing sporophyte, and bearing the perianth and female bracts. See Paton 1999: 276, 286, and 331 for illustrations.)

Nine species in California.

Species Key

Plants with perianths are more easily keyed to species than are vegetative only plants. However, most collections will consist only of vegetative plants. The first key is for plants with perianths. For vegetative plants, go directly to the second key.

1. Key to Plants with Perianths

1. Perianth cylindrical, smooth (not plicate), and abruptly contracted near the apex to a short tubular beaked mouth recessed in a shallow apical depression; leaves oblong, ± parallel-sided. . . . . **J. leiantha**
1. Perianth cylindrical, smooth below, plicate above, and gradually or abruptly contracted near the apex to a non-beaked or beaked mouth (if beaked, the beak not recessed in an apical depression); leaves various, but not oblong and ± parallel-sided. . . . . **2.**
2. Perigynium half as long or longer than the perianth; perianth emergent 0.5 or less its length beyond the female bracts. . . . . **3.**
2. Perigynium absent or very short; perianth usually long-emergent. . . . . **4.**
3. Leaves clearly bordered with thick-walled marginal cells (marginal leaf cells clearly differentiated from inner cells). . . . . **J. rubra**
3. Leaves not clearly bordered with thick-walled marginal cells (marginal leaf cells often not or little differentiated from inner cells). . . . . **J. hyalina**
4. Perigynium usually absent; perianth long-exserted above the female bracts, the bracts not sheathing the base of the perianth; perianth gradually narrowed to a non-beaked mouth; rhizoids from the stem only. . . . . **5.**
4. Perigynium usually present, but very low; perianth exserted above the female bracts by ½ to ¾ its length, the bracts sheathing the base of the perianth; perianth rather abruptly contracted near the apex to a short beaked mouth; rhizoids from both the stem and leaf base. . . . . **8.**
5. Dioicous. . . . . **6.**
5. Paroicous. . . . . **7.**
6. Plants usually blackish-green, 10 cm or more long; aromatic when fresh; leaves usually flacid, cordate to triangular and obtuse to broadly rounded at the apex. . . . . **J. exsertifolia** subsp. **cordifolia**
6. Plants usually olive- to yellowish-green, up to 4 cm long; not aromatic when fresh; leaves not flaccid, mostly ovate and broadly rounded at the apex. . . . . **J. atrovirens**
7. Median leaf cells mostly 17–28 μm wide × 25–30 μm long (or longer); perianths gradually narrowed to apex (fusiform), especially when young. . . . . **J. pumila**

7. Median leaf cells mostly 12–20 μm wide × 16–25 μm long; perianths widest near middle and rather abruptly rounded to apex. . . . . **J. polaris**
8. Leaves mostly reniform; rhizoids often in clusters from both stem and leaf base, with many closely appressed to the stem; in sun-forms the leaf margins, bracts and perianths often with pinkish, reddish, or purplish pigmentation. . . . . **J. confertissima**
8. Leaves nearly circular; rhizoids not in clusters with few from the leaf base and mostly oriented perpendicular to the stem; in sun-forms the leaves, bracts and perianths with brownish, never reddish coloration. . . . . **J. sphaerocarpa**

2. Key to Vegetative Plants

1. Leaves usually oblong and more-or-less parallel-sided; occasionally with attenuated gemmiferous shoots. . . . . **J. leiantha**
1. Leaves various, but not oblong and parallel-sided; gemmae and gemmiferous shoots always absent. . . . . **2.**
2. Leaves clearly bordered with thick-walled marginal cells (marginal leaf cells clearly differentiated from inner cells). . . . . **J. rubra**
2. Leaves not clearly bordered with thick-walled marginal cells (marginal leaf cells often not or little differentiated from inner cells). . . . . **3.**
3. Rhizoids (at least some) developing from leaf bases as well as stem tissue. . . . . **4.**
3. Rhizoids developing only from stem tissue. . . . . **6.**
4. Leaves obliquely inserted and nearly horizontal near the dorsal stem surface, usually long decurrent on the dorsal stem surface, and nearly semi-circular and widest near the base. . . . . **J. hyalina**
4. Leaves obliquely inserted but not nearly horizontal near the dorsal stem surface, not or short decurrent on the dorsal stem surface, and nearly circular or reniform and widest near the middle. . . . . **5.**
5. Leaves mostly reniform; rhizoids often in clusters from both the stem and leaf base, with many closely appressed to the stem; in sun-forms the leaf margins, bracts and perianths often with pinkish, reddish or purplish pigmentation. . . . . **J. confertissima**
5. Leaves nearly circular; rhizoids not in clusters, with a few from the leaf base and most oriented perpendicular to the stem; in sun-forms the leaves, bracts and perianths with brownish, never reddish coloration. . . . . **J. sphaerocarpa**
6. Shoots large, 2–12 cm long, usually blackish green; living plants strongly aromatic; leaves flaccid; rhizoids few, mostly near stem bases. . . . . **J. exsertifolia** subsp. **cordifolia**
6. Shoots usually less than 4 cm long, olive-green to blackish; living plants aromatic or not; leaves not flaccid; rhizoids numerous, nearly to the stem apex. . . . . **7.**
7. Plants small, less than 1 mm wide; median leaf cells 12–20 μm wide × 16–25 μm long. . . . . **J. polaris**
7. Plants larger, to 4.5 mm wide; median leaf cells 15–30 μm wide × 20–35 μm long or longer (At times, vegetative plants of the following two species can be impossible to separate.) . . **8.**
8. Typical, robust plants mostly with broadly ovate leaves; oil-bodies 2–3 per leaf cell; living plants aromatic. . . . . **J. atrovirens**
8. Typical, robust plants with somewhat elliptical leaves; oil-bodies 4–5 per leaf cell; living plants not aromatic. . . . . **J. pumila**

Jungermannia atrovirens Dumort.

Distinctive features. This dioicous species grows in yellowish-, olive-, to blackish-green populations. Look for a) shoots 0.5–4.5 mm wide, b) living plants aromatic, c) leaves often broadly ovate, d) median leaf cells thin-walled, mostly 15–25 μm wide and 20–33 μm long, e) leaf marginal cells mostly 10–15 μm wide, f) rhizoids from the stem surface, none from the leaf base, g) oil-bodies mostly 2–3 per leaf cell, and h) perianths oblong to cylindrical, plicate and narrowed toward the apex to a non-beaked mouth.

Separation. Jungermannia atrovirens and *J. pumila* share many characteristics and are most easily separated when reproductive: *J. atrovirens* is dioicous whereas *J. pumila* is paroicous. Because of morphological variability of vegetative plants, some populations of the two species can be impossible to identify with absolute certainty. Mature "typical" vegetative plants of *J. atrovirens* can be separated from those of *J. pumila* mainly by a) leaves often broadly ovate (vs. leaves rather elliptical in *J. pumila*), b) living plants aromatic (vs. living plants not aromatic), and c) oil-bodies 2–3 per median leaf cell (vs. oil-bodies mostly 4–5 per median leaf cell).

Illustrations. Damsholt 2002 (as *J. lanceolata*); Paton 1999; Schuster 1969; Smith 1990.

Habitat. On soil and rocks in wet places, such as stream banks where often seasonally submerged. Elevation from 115 to 2000 m.

Distribution. Jungermannia atrovirens occurs in Europe, Asia, Africa, and North America. Calif. Geographic Regions: **KR**: Del Norte Co. *Doyle 11068* (perianths) (UC).

Jungermannia confertissima Nees

Distinctive features. This usually erect paroicous species often occurs in yellowish-green to green populations. The leaves of sun-forms, however, can be pink, reddish or purplish toward the margins (the leaf bases and stems are not reddish). Look for a) leaves reniform, obliquely to subtransversely inserted, b) median leaf cells mostly 25–35 μm wide × 25–42 μm long, c) marginal leaf cells 24–30 μm wide, d) rhizoids numerous, brownish, hyaline or occasionally purplish, often in clusters from stem and leaf bases, with many rhizoids closely appressed to the stem, and e) perianths of sun-forms usually reddish or purplish.

Separation. This species can be confused with *J. sphaerocarpa*, however, *J. confertissima* can be separated by a) leaves subtransversely inserted, reniform and concave (vs. leaves obliquely inserted, not reniform and little or not concave and often spreading in *J. sphaerocarpa*), b) rhizoids mostly appressed to the stem (vs. rhizoids mostly at right angles to the stem), and c) leaf margins and perianths occasionally with reddish or purplish pigmentation (vs. leaf margins and perianths brownish; rarely, if ever, reddish or purplish).

Illustrations. Damsholt 2002; Paton 1999; Schuster 1969; Smith 1990.

Habitat. On shaded, damp stream banks and rocks. Elevation above 1100 m.

Distribution. Jungermannia confertissima occurs in Europe, Asia, and North America. Calif. Geographic Regions: **SN**: Tulare Co. *Doyle 2855* (perianths) (UC).

Jungermannia exsertifolia Steph. subsp. ***cordifolia*** (Dumort.) Váňa

Distinctive features. This gray- to blackish-green dioicous species consists of large plants, up to 18 cm long. Look for a) living plants aromatic, b) leaf bases loosely sheath the stem, c) median leaf cells 20–30 μm wide × 30–60 μm long, with dark brown to blackish-brown walls, d) rhizoids hyaline to brownish, only from the stem, and e) perianths long-exserted, fusiform, plicate near the apex and narrowed to a non-beaked mouth.

Separation. With its large size, aromatic living plants, sheathing leaf bases, brown to blackish-brown leaf cell walls, and sparse development of rhizoids, *J. exsertifolia* subsp. *cordifolia* should not be confused with other California species of *Jungermannia.*

Illustrations. Damsholt 2002; Paton 1999; Schuster 1969; Smith 1990.

Habitat. Usually attached to rocks in or near swiftly flowing water, where it is seasonally submerged. Elevation from 1800 to 3050 m.

Distribution. Jungermannia exsertifolia subsp. *cordifolia* occurs in Europe, Asia, and North America. Calif. Geographic Regions: **CR**: Shasta Co. *Doyle 9314* (UC), **KR**: Trinity Co. *Doyle 6046* (perianths) (UC), **SC**: San Bernardino Co. *Howell 719* (CAS), **SN**: Nevada Co. *Norris 102605* (UC).

Jungermannia hyalina Lyell

Distinctive features. This species usually is green to yellow-green. Look for a) nearly semi-circular leaves about as wide as long, and widest at or near the leaf base, b) leaves usually clearly decurrent on the dorsal stem surface, c) median leaf cells 25–35 μm wide × 30–45 μm long, and marginal leaf cells 21–35 μm wide, d) rhizoids brownish to reddish (seldom hyaline), mostly from the stem, but some from the leaf base, e) leaf bases and the ventral sides of stems often reddish, f) stem epidermal cells thin-walled, 5–10 times as long as wide, and g) oil-bodies 2–5 per leaf cell.

Separation. This species can be confused with *J. confertissima* and *J. sphaerocarpa*. It is separated from both by nearly semicircular leaves that are widest at or near the leaf base (vs. reniform or nearly circular leaves that are widest near the leaf middle.

Illustrations. Damsholt 2002; Paton 1999; Schuster 1969; Smith 1990.

Habitat. On mineral and peaty soil; drainages through meadows, along streams. Elevation from 1800 to 2500 m.

Distribution. Jungermannia hyalina occurs in Europe, Asia, North Africa, and North America. Calif. Geographic Regions: **SN**: Fresno Co. *Doyle 10728* (male plants) (UC).

Jungermannia leiantha Grolle

Distinctive features. These paroicous plants, with shoots 2–2.5 mm wide, occur mostly in green to yellowish-brown patches. Look for a) leaves often nearly parallel-sided with rounded apices, b) median leaf cells 28–33 μm wide × 30–50 μm long, c) leaf cells thin-walled with small to bulging trigones, d) older leaves usually with brownish cell walls, e) oil-bodies granular, mostly 7–11 per leaf cell, f) rhizoids hyaline or pale brownish, g) underleaves absent, and h) perianth smooth (not plicate), abruptly contracted near the apex into a short, tubular beak that is recessed in a shallow depression.

Separation. The cylindrical perianth abruptly contracted near the apex into a short, tubular beak recessed in a shallow depression clearly separates *J. leiantha* from other members of the genus. Vegetative plants of *J. leiantha* are separated from *Mylia anomala* by the absence of underleaves (underleaves present in *M. anomala*).

Illustrations. Damsholt 2002 (as *J. subulata*); Frye and Clark 1943 (as *J. lanceolata*); Schuster 1969 (as *J. lanceolata*).

Habitat. Generally on moist decaying logs in seepages and near creeks, and on peaty substrates. Elevation from 200 to 3050 m.

Distribution. Jungermannia leiantha occurs in Europe and North America. Calif. Geographic Regions: **CR**: Tehama Co. *Doyle 11102* (perianths) (UC), **KR**: Siskiyou Co. *Shevock 26194* (CAS), **MP**: Modoc Co. *Doyle 6687* (gemmae and perianths) (UC), **SN**: Tulare Co. *Doyle 7807* (perianths) (UC).

Jungermannia polaris Lindb.

Distinctive features. This small, paroicous plant occurs in yellowish- to dark- to blackish-green patches. Look for a) shoots less than 1 mm wide, b) leaves concave, broadly ovate to round, c) median leaf cells thin-walled 12–20 μm wide × 16–25 μm long, with small trigones, d) oil-bodies mostly 2–4 per leaf cell, and e) perianths nearly pyriform, smooth below and rounded and plicate from about the middle to a non-beaked mouth.

Separation. Both *J. polaris* and *J. pumila* are morphologically variable and some populations can be difficult to identify. Most of the time, *J. polaris* can be separated by one or more of the following a) shoots less than 1 mm wide (vs. shoots usually more than 1 mm and up to 3.5 mm wide in *J. pumila*), b) leaves broadly ovate to round (vs. leaves mostly elliptical), c) median leaf cells 12–20 μm wide × 16–25 μm long (vs. median leaf cells 17–28 μm wide × 25–35 μm long), and d) mature perianths mostly pyriform (vs. mature perianths usually fusiform).

Illustrations. Damsholt 2002; Paton 1999; Schuster 1969; Smith 1990.

Habitat. Near streams. Elevation from 3000 to 3500 m.

Distribution. Jungermannia polaris occurs at high elevations in Europe, Asia, and North America. Calif. Geographic Regions: **SN**: Mono Co. *Doyle 10263* (perianths) (UC).

Jungermannia pumila With.

Distinctive features. Populations of this paroicous species vary from olive-to dark to blackish-green. Look for a) living plants non-aromatic, b) shoots 0.5–3.5 mm wide, c) leaves generally elliptical to ovoid, d) leaf cells thin-walled with no or only small trigones, e) median leaf cells 17–28 μm wide × 25–35 μm long, f) rhizoids from the stem surface, none from the leaf base, g) oil-bodies mostly 4–5 per leaf cell, and h) perianth usually somewhat fusiform and slightly flattened, narrowed and plicate toward the apex, with a non-beaked mouth.

Separation. Jungermannia pumila (paroicous) and *J. atrovirens* (dioicous) are definitively separated on the basis of sexuality. Vegetative plants, however, sometimes cannot be identified with certainty.

See *J. atrovirens* for a possible separation from that species. See *Jungermannia pumila* for separation from that species.

Illustrations. Damsholt 2002; Paton 1999; Schuster 1969; Smith 1990.

Habitat. On rocks near streams where it is seasonally submerged. Elevation from 2100 to 2600 m.

Distribution. Jungermannia pumila occurs in Europe, Asia, Africa, and North America. Calif. Geographic Regions: **KR**: Del Norte Co. *Doyle 2040* (large aquatic form; perianths) (UC), **SN**: Madera Co. *Doyle 6915* (perianths) (UC).

Jungermannia rubra Gottsche ex Underw.

Distinctive features. These dioicous plants often grow in large patches. The shoots generally are green when actively growing and in damp shaded habitats, and reddish in exposed and drying habitats. Look for a) leaves usually bordered with thick-walled marginal cells usually slightly larger than the submarginal cells (**note**—the extent of wall thickening of marginal cells is variable), b) median leaf cells with distinct and often bulging trigones, c) rhizoids hyaline, and d) perianths plicate, reddish to purplish, with a beaked mouth.

Separation. Jungermannia rubra is separated from other species of *Jungermannia* by the following combination of features a) reddish shoot coloration, b) marginal leaf cells thick-walled, c) median leaf cells with distinct trigones, d) a perigynium present, and e) perianths reddish to purplish.

Illustrations. Frye and Clark 1943; Schofield 2002.

Habitat. Soil, occasionally on rocks; shaded banks, hillsides and cliffs; near sea-level to 2160 m; usually below 1110 m.

Distribution. Jungermannia rubra occurs in western North America. Calif. Geographic Regions: **CC**: San Mateo Co. *Doyle 10394* (UC), **CR**: Shasta Co. *Doyle 10985* (UC), **KR**: Trinity Co. *Norris 99804* (UC), **MP**: Modoc Co. *Doyle 9659* (UC), **NC**: Humboldt Co. *Doyle 10056* (UC), **SC**: Riverside Co. *Doyle 7336* (UC), **SN**: Yuba Co. *Doyle 9575.*

Jungermannia sphaerocarpa Hook.

Distinctive features. This paroicous species often occurs in green patches or olive-green to brownish patches in exposed sun-forms. Look for a) leaves nearly circular (orbicular) that are obliquely to sub-transversely inserted and widest near the leaf middle, b) leaves occasionally slightly bordered, with median leaf cells 22–32 μm wide × 30–40 μm long and marginal cells 16–24 μm wide, c) rhizoids hyaline to brownish, mostly from the stem, but a few from the leaf base, d) rhizoids mostly oriented perpendicular to the stem, and d) perianths and bracts without reddish or purplish coloration.

Separation. This species can be confused with *J. confertissima*. For separation, see discussion under that species.

Illustrations. Damsholt 2002; Paton 1999; Schuster 1969; Smith 1990.

Habitat. On rocks and soil of creek banks. Elevation up to 3000 m.

Distribution. Jungermannia sphaerocarpa occurs in Europe, Asia, and North and South America. Calif. Geographic Regions: **SN**: Tuolumne Co. *Doyle 10316* (perianths) (UC).

Kurzia G. Martens 1870
(Lepidoziaceae)

This is a genus of small plants, less than 0.5 mm wide. Look for a) leaves transversely inserted on the stem, b) leaves divided nearly to base into 3–4 lobes, and c) underleaves smaller than the leaves and divided nearly to the base into 3–4 lobes.

One species in California.

Kurzia sylvatica (A. Evans) Grolle

Distinctive features. This is a very small plant and easily overlooked except when growing in mats. The brownish-green to yellowish-brown shoots are less than 0.4 mm wide. Look for a) leaves transversely inserted and usually overlapping, b) stem leaves symmetrically 3–4 lobed; the dorsal leaf

lobe equal in size to the ventral lobe, c) leaf lobes each with 2–3 superposed cells at the tip and 2–3 cells wide at the base, d) underleaves 3–4 lobed with 1–2 lobes markedly reduced in size to only one or two cells long, and e) oil-bodies usually absent from all leaf cells.

Separation. With its a) small size (less than 0.4 mm wide), b) leaves deeply divided into 3–4 lobes, c) leaf lobes uniseriate at the tip and 2–3 cells wide at the base, and underleaves lobed and smaller than the leaves, this species is easily separated from all other California liverworts. *Blepharostoma* and *Lepidozia* also have deeply divided leaves and underleaves, but *Blepharostoma* has leaf and underleaf lobes uniseriate to the base, and *Lepidozia* has leaves and underleaves divided for only 0.5 their length.

Kurzia sylvatica can be confused with *K. makinoana* (Steph.) Grolle, a species of East Asia that has not been collected in California. *Kurzia sylvatica* can be separated by a) stem leaves usually overlapping (vs. stem leaves usually somewhat remote in *K. makinoana*), b) stem leaves symmetrical, with the dorsal leaf lobe as large as the ventral leaf lobe (vs. stem leaves asymmetrical, with the dorsal leaf lobe smaller [often spinose] than the ventral leaf lobe), and c) underleaves asymmetrical with 1–2 lobes markedly reduced or aborted (vs. underleaves usually symmetrical or with only one lobe slightly smaller in size).

Illustrations. Damsholt 2002; Paton 1999; Schuster 1969.

Habitat. On shaded, moist, decaying logs and hummocks, especially in *Sphagnum* bog areas. Elevation from near sea-level to 35 m.

Distribution. Kurzia sylvatica occurs in Europe and North America. Calif. Geographic Regions: **NC**: Humboldt Co. *Doyle 10582* (UC); Mendocino Co. *Doyle 10502* (UC).

Lepidozia (Dumort.) Dumort. 1835
(Lepidoziaceae)

Plants of this genus are dark to yellowish-green and regularly 1–2 pinnately branched. Look for a) leaves 3–5-lobed, divided for 0.5 their length or less, b) underleaves 3–4-lobed, divided for less than 0.5 their length, c) oil-bodies 5–10 per leaf cell, and d) flagelliform branches present.

One species in California.

Lepidozia reptans (L.) Dumort.

Distinctive features. Mature shoots of this autoicous species are over 1 mm wide. Look for a) leaves on main stems divided up to 0.5 their length into 3–4 triangular lobes, with incurved lobe tips, b) the undivided leaf base 4–7 cells wide, c) underleaves divided up to 0.5 their length into 3–4 lobes, d) oil-bodies 10–16 per leaf cell, and d) flagelliform branches with small leaves.

Separation. This distinctive species is not easily confused with other California liverworts. See *Kurzia sylvatica* for separation from that species.

Illustrations. Damsholt 2002; Paton 1999; Schofield 2002; Schuster 1969; Smith 1990.

Habitat. Shaded, damp decaying logs and stumps, and base of trees in redwood forests. Elevation from 25 to 200 m.

Distribution. Lepidozia reptans occurs in Europe, Asia, and North America. Calif. Geographic Regions: **CC**: San Mateo Co. *Doyle 10369* (UC), **KR**: Del Norte Co. *Doyle 7722* (UC), **NC** Sonoma Co. *Doyle 10654* (UC).

Lophocolea (Dumort.) Dumort. 1835
(Geocalycaceae)

This genus is characterized by a) perianths terminal on the main stem or short lateral branch, b) succubous leaves, c) some or all leaves bilobed, d) underleaves bilobed, with lobes usually spreading, and e) rhizoids in clusters and restricted to the underleaf base.

Some researchers (e.g., Damsholt 2002; Schuster 1969) include *Lophocolea* within the genus *Chiloscyphus*. The traditional recognition of these two as separate genera is followed here, in part based on a) perianth terminal on the main stem or short lateral branch (vs. perianth usually terminal on a dwarf lateral branch in *Chiloscyphus*), b) leaves either bilobed throughout or at least some leaves

shallowly bilobed (vs. leaves entire or emarginate, c) underleaf lobes spreading, with rather large teeth on the lateral margins (vs. underleaves usually with somewhat parallel-sided lobes, with no or smaller, less conspicuous lateral teeth). See also Grolle (1995) for reasons to maintain *Lophocolea* and *Chiloscyphus* as separate genera.

Two species in California. This publication follows Smith (1990) and Paton (1999) in including *L. cuspidata* within the circumscription of *L. bidentata*.

Species Key

1. Leaves polymorphic, even on same shoot, entire, slightly indented or shallowly bilobed; lobe apices rounded to obtuse. . . . . **L. heterophylla**
1. Leaves clearly bilobed throughout; lobe apices acute to acuminate, terminated by 2–6 uniseriate cells. . . . . **L. bidentata**

Lophocolea bidentata (L.) Dumort.

Distinctive features. These dioicous or autoicous, whitish- to yellowish-green plants are 2–3.5 mm wide. Look for a) leaves distinctly bilobed with the lobe apices ending in 2–6 uniseriate cells, b) underleaves deeply bifid, up to 0.8 their length, and c) perianths terminal on long branches.

Separation. This species is not easily confused with other California leafy liverworts.

Illustrations. Damsholt 2002; Paton 1999; Schofield 2002 (as *L. cuspidata*); Schuster 1969; Smith 1990.

Habitat. Wet, humid habitats; usually on decaying wood and organic matter; occasionally on soil and base of trunks of living trees. Elevation from 25 to 1650 m; mostly below 850 m.

Distribution. Lophocolea bidentata occurs in Europe, Africa, Asia, and North America. Calif. Geographic Regions: **CC** San Francisco Co. *Shevock 19306* (CAS), **KR**: Trinity Co. *Doyle 4652* (UC), **NC**: Humboldt Co. *Doyle 11074* (UC), **SN**: Yuba Co. *Doyle 9585* (UC).

Lophocolea heterophylla (Schrad.) Dumort.

Distinctive features. This paroicous species usually occurs in green to yellowish-green patches. The shoots are 1–1.8 mm wide. As the name implies, this is a morphologically variable species. Look for a) leaves entire, emarginate, retuse, and/or shallowly bilobed often on the same stem (examine leaves from several areas of the population), b) underleaves bifid to below their middle, and c) perianths terminal on short branches.

Separation. The small shoot width, 1–1.8 mm, and polymorphic leaf apices separate this species from *L. bidentata*.

Illustrations. Damsholt 2002; Paton 1999; Schuster 1969; Smith 1990.

Habitat. Usually on shaded decaying logs and wood; occasionally on soil. Elevation from 20 to 1485 m; mostly below 760 m.

Distribution. Lophocolea heterophylla occurs in Europe, Africa, Asia, and North America. Calif. Geographic Regions: **CC**: San Mateo Co. *Doyle 10372* (UC), **CR**: Tehama Co. *Doyle 8764* (UC), **KR**: Del Norte Co. *Doyle 7748* (UC), **NC**: Humboldt Co. *Doyle 10070* (UC), **SN**: Yuba Co. *Dillingham 986* (CHSC).

Lophozia (Dumort.) Dumort. 1835
(Scapaniaceae)

This is a large, heterogeneous and often difficult genus. Species identification becomes easier with experience. As treated in this publication, plants included in *Lophozia* have a) leaves mostly obliquely inserted, b) leaves predominantly bifid (although a few species have both 2- and 3-lobed leaves on the same stem; and another species has 3–4-lobed leaves), c) leaves lacking uniseriate filaments on the ventral base, and d) gemmae angular, stellate or tetrahedral.

Because of environmentally-induced morphological variations that can blur lines among species, a combination of features often must be used to identifiy some specimens. Careful observations and

measurements on healthy, mature vegetative plants, gemmae, and perianths contribute to the security of correct species identification.

In this treatment we have not recognized *Leiocolea* as a genus distinct from *Lophozia*, as also reflected in Appendix II. However, recent studies such as that of Forrest et al. (2006) show that *Leiocolea* is phylogenetically quite removed from *Lophozia*. Four of the species treated here, namely, *L. bantriensis, L. collaris, L. gillmanii*, and *L. heterocolpos*, should perhaps be regarded as species of the genus *Leiocolea*, rather than *Lophozia*.

Eleven species plus one variety in California; one species to be described.

Species Key

1. Underleaves linear, subulate or lanceolate frequently to usually present on vegetative stems. **2.**
1. Underleaves absent, infrequent, or very small. . . . . **6.**
2. Leaf lobes clearly rounded; median leaf cells isodiametric; oil-bodies 15–50 per cell. **L. obtusa**
2. Leaf lobes acute to subacute; median leaf cells slightly to much longer than wide; oil-bodies 2–10 per cell. . . . . **3.**
3. Gemmae brown, on leaf margins of erect attenuated stems; median cells of mature leaves with large bulging trigones. . . . . **L. heterocolpos**
3. Gemmae lacking and erect attenuated shoots not present; median leaf cells mostly with small to moderate trigones (rarely bulging). . . . . **4.**
4. Paroicous; perianths usually rather long-beaked. . . . . **L. gillmanii**
4. Dioicous; perianths mostly not or only short-beaked. . . . . **5.**
5. Leaves clearly decurrent on the dorsal stem surface; median leaf cells 35–40 μm wide; mature shoots 3–4 mm wide. . . . . **L. bantriensis**
5. Leaves not or slightly decurrent on the dorsal stem surface; median leaf cells 25–30 μm wide; mature shoots 1–2.8 mm wide. . . . . **L. collaris**
6. Plants small, less than 1 mm wide; stems translucent; perianths smooth (not plicate), abruptly contracted near the apex to a distinct beak. . . . . **L.**, sp. nov.
6. Plants larger, usually 1–3 mm wide; stems not translucent; perianths usually smooth below but plicate toward the mouth, not-beaked. . . . . **7.**
7. Plants pale bluish-green; leaves near the shoot apex usually 3–5 lobed and often with marginal teeth; leaves rather opaque; oil-bodies 20–50 per leaf cell. . . . . **8.**
7. Plants green, yellowish- to reddish-brown, or brown; leaves near the shoot apex usually 2-lobed; leaves seldom opaque; oil-bodies 4–24 per leaf cell. . . . . **9.**
8. Leaves near the shoot apex usually spinose; leaf lobes broadly triangular; plants of higher elevation, usually over 2000 m. . . . . **L. incisa** var. **incisa**
8. Leaves near the shoot apex not spinose; leaf lobes more narrowly triangular; plants of lower elevation, below 2000 m. . . . . **L. incisa** var. **opacifolia**
9. Gemmae reddish-brown, reddish-purple or purple. . . . . **10.**
9. Gemmae pale or yellow green. . . . . **12.**
10. Leaf cell walls often strongly brownish; trigones of leaf cells distinct to moderately bulging; gemmae reddish-brown. . . . . **L. sudetica**
10. Leaf cell walls colorless (but brownish, purplish-brown or tinged reddish in sun-exposed plants); trigones of leaf cells absent or small; gemmae vinaceous, purplish or brownish-purple. . . . . **11.**
11. Paroicous; gemmae pyramidal to 5-angled; sun-exposed plants often with reddish to purplish pigmentation. . . . . **L. excisa**
11. Dioicous; gemmae irregularly pyriform; sun-exposed plants often with brownish pigmentation. . . . . **L. latifolia**
12. Leaves as long as or longer than wide; median leaf cells with large bulging trigones; perianth mouth with teeth 2–5 cells long. . . . . **L. longiflora**
12. Leaves as wide as or wider than long; median leaf cells with concave to moderately bulging trigones; perianth mouth with teeth mostly 1–2 cells long. . . . . **13.**
13. Leaves concave with incurved lobe margins and shallowly bilobed to 0.2 their length with wide, usually with crescentic sinuses. . . . . **L. wenzelii**
13. Leaves flat or weakly concave, lacking incurved lobe margins and bilobed 0.2–0.3 their length with obtuse to rectangular sinuses. . . . . **L. ventricosa**

Excluded. Lophozia obtusa (Lindb.) A. Evans. Based on *Howell 586* (CAS), Sutliffe (1942) reported *Lophozia (Leiocolea) obtusa* from Madera Co., Sierra Nevada. This specimen, as well as *Howell 603* (CAS) from Tulare Co., was mis-identified. No specimens of *L. obtusa* were located during this study.

It could not be confirmed for California. (Descriptions and illustrations of this species occur in Schuster 1969, Smith 1990, Paton 1999, and Damsholt 2002).

Lophozia bantriensis (Hook.) Steph.

Distinctive features. These green to reddish-brown to blackish plants are 3–4 mm wide × 2–5 cm long or longer. Look for a) underleaves lanceolate (rarely bilobed) with marginal teeth, b) leaves flaccid, often convex, divided to 0.25 their length into acute to obtuse lobes, c) median leaf cells usually thin-walled, 35–40 µm wide × 40–60 µm long with small to moderate trigones, c) oil-bodies brownish, 2–4 pale per cell, d) gemmae lacking, and e) perianths cylindrical below, abruptly contracted and often plicate near the apex to a nonbeaked or short beaked mouth (the perianth mouth often is somewhat obliquely positioned).

Separation. The consistent presence of underleaves easily separates this species from others in the genus, except for *L. collaris, L. gillmanii* and *L. heterocolpos*. See *L. heterocolpos* for separation from that species. *L. bantriensis* and *L. gillmanii* are nearly the same size, have similar leaf cell sizes and have similar underleaves. Vegetative shoots can be impossible to identify with certainty. The two species consistently differ only in sexuality—*L. bantriensis* is dioicous and *L. gillmanii* is paroicous.

Lophozia bantriensis and *L. collaris* both are dioicous and share similar leaf and underleaf form. *Lophozia bantriensis* can be separated by the larger median leaf cells 35–40 µm wide × 40–60 µm long (vs. median leaf cells 25–30 µm wide × 27–35 µm long in *L. collaris*).

Illustrations. Damsholt 2002; Paton 1999; Schuster 1969; Smith 1990.

Habitat. On shaded moist soil near springs, marshes, stream banks, etc. Elevation from 2000 to 3200 m.

Distribution. Lophozia bantriensis occurs in Europe, Asia, and North America. Calif. Geographic Regions: **KR**: Del Norte Co. *Doyle 9763* (UC), **SN**: Mono Co. *Whittemore 1537A* (perianths) (CAS).

Lophozia collaris (Nees) Dumort.

Distinctive features. These often brownish dioicous plants are 1–2.8 mm wide and 0.8–3.5 cm long. Look for a) underleaves lanceolate, usually with 2–4 marginal filaments or slime hairs, b) median leaf cells 25–30 µm wide × 27–34 µm long, b) oil-bodies grayish, 2–5 per median leaf cell, c) gemmae lacking, and d) perianths cylindrical, abruptly contracted near the apex into a short beaked mouth, the mouth with elongate 1–2-celled teeth.

Separation. The consistent presence of underleaves separate this species from others in the genus, except for *L. bantriensis, L. gillmanii* and *L. heterocolpos. L. collaris* is separated from a) *L. heterocolpos* by sexuality (doicous) and absence of gemmae development (vs. paroicous and reddish-brown gemmae on specialized erect shoots), b) *L. gillmanii* by sexuality (dioicous) and smaller median leaf cell size, 25–30 µm wide (vs. paroicous and median leaf cell size 30–36 µm wide), and c) from *L. bantriensis* by smaller median leaf cell size, 25–30 µm wide (vs. median leaf cell size 35–40 µm wide).

Illustrations. Damsholt 2002; Paton 1999; Schuster 1969; Smith 1990.

Habitat. On soil and rocks of creek banks. Elevation from 1450 to 3000 m.

Distribution. Lophozia collaris occurs in Europe, Asia, and North America. Calif. Geographic Regions: **SN**: Nevada Co. *Whittemore 4157* (CAS).

Lophozia excisa (Dicks.) Dumort.

Distinctive features. These frequently fertile paroicous plants are variable in size and appearance. Shoots often have a pale green color, but in exposed sun-forms, the shoots often are tinged reddish or purplish. Shoots are 1.0–2.3 mm wide × 0.5–3 cm long. Look for a) leaves bilobed with broadly triangular lobes and somewhat crisped leaves near the shoot apex, b) leaves short decurrent on the dorsal stem surface, c) median leaf cells thin-walled, 20–32 µm wide × 28–40 µm long, with no or very small trigones, d) stems somewhat fleshy, e) oil-bodies 11–18 per leaf cell, f) underleaves absent (or rare), g) gemmae vinaceous to reddish-brown, bluntly angular to polyhedral with rounded thick-walled angles, and h) perianth plicate above and contracted to a non-beaked and shallowly lobed mouth, with a crenulate margin.

Separation. This species can be confused with *L. latifolia*, *L. sudetica* and *L. ventricosa*. See *L. latifolia* for separation from that species. See *L. sudetica* for separation from that species. *Lophozia excisa* can be separated from *L. ventricosa* by a) being paroicous (vs. dioicous in *L. ventricosa*), b) gemmae vinaceous to reddish-brown (vs. gemmae greenish), and c) leaves near the shoot apex somewhat crisped (vs. leaves near the shoot apex not crisped).

Illustrations. Damsholt 2002; Paton 1999; Schuster 1969; Smith 1990.

Habitat. On organic matter. Elevation under 500 m.

Distribution. Lophozia excisa occurs in Europe, Asia, Antarctica, South Pacific, and North and South America. Calif. Geographic Regions: **NC**: Humboldt Co. *Boratynski 213* (CHSC).

Lophozia gillmanii (Austin) R. M. Schust.

Distinctive features. This paroicous species usually is pale- to deep- to blackish-green, 1–4 mm wide × 2–4 cm long. Look for perianths and determine whether the population is paroicous or dioicous. Look for a) underleaves subulate or lanceolate; search near the stem apex because they are small and often are obscured by the dense growth of rhizoids in older stem areas, b) median leaf cells usually 30–36 μm wide × 36–50 μm long, usually with coarse to strongly bulging trigones, c) gemma absent, and d) perianths cylindrical, abruptly contracted (but not plicate) near the apex into a rather elongate beaked mouth (the elongate beak can be easily broken off; observe perianths carefully to be sure that a "non-beaked" mouth is intact, rather than represented by broken perianth cells).

Separation. The consistent presence of underleaves separates this species from others in the genus, except for *L. bantriensis, L. collaris*, and *L. heterocolpos. Lophozia gillmanii* is separated from *L. heterocolpos* by a) gemma development absent (vs. gemmae on erect specialized branches in *L. heterocolpos*), and b) larger median leaf cells, 30–36 μm wide × 36–50 μm long (vs. median leaf cells 20–27 μm wide × 22–36 μm long). *Lophozia gillmanii* is separated from *L. bantriensis,* and *L. collaris* by being paroicous (vs. dioicous), and, additionally, from *L. collaris* by larger median leaf cells 30–36 μm wide (vs. median leaf cells 25–30 μm wide in *L. collaris*).

Illustrations. Damsholt 2002; Paton 1999; Schofield 2002; Schuster 1969; Smith 1990.

Habitat. Soil of creek banks. Elevation above 1500 m.

Distribution. Lophozia gillmanii occurs in Europe, Asia, and North America. Calif. Geographic Regions: **SN**: Tulare Co. *Doyle 7839* (UC).

Lophozia heterocolpos (Thed. ex. Hartm.) M. Howe

Distinctive features. These green (in shade) to warm brown (in sun) dioicous plants are 1.5–3.0 mm wide × 0.8–1.5 cm long. They have smooth cylindrical perianths that are abruptly contracted near the apex to a short beak and toothed mouth. Gemmae development is distinctive and some plants of a population usually have gemmae. Look for erect, somewhat stiff, slender gemmiferous shoots with brownish gemmae that develop mostly from brownish leaf margins. The 2-celled gemmae are smooth (not angular). Also look for a) leaf cells thin- to moderately thick-walled, usually with large convex, often confluent trigones, b) cell walls and trigones often a warm brown in color, c) median leaf cells 20–27 μm wide × 22–36 μm long, d) underleaves lanceolate (especially visible near the shoot apex), usually with cilia or slime papillae on the lateral margins, and e) 2–5 oil-bodies per leaf cell.

Separation. The consistent presence of underleaves separates this species from others in the genus, except for *L. bantriensis. L. collaris* and *L. gillmanii*. None of these three species, however, have the specialized erect gemmiferous shoots with smooth brownish gemmae that almost always are present in *L. heterocolpos*.

Illustrations. Damsholt 2002; Paton 1999; Schuster 1969; Smith 1990.

Habitat. Shaded soil in drainages, base of cliffs and near streams. Elevation from 1400 to 3350 m.

Distribution. Lophozia heterocolpos occurs in Europe, Asia, and North America. Calif. Geographic Regions: **KR**: Siskiyou Co. *Doyle 9234* (UC), **MP**: Modoc Co. *Doyle 6685* (UC), **SN**: Alpine Co. *Doyle 8824* (UC).

Lophozia incisa (Schrad.) Dumort. subsp. **incisa**

Distinctive features. This distinctive dioicous species often can be recognized in the field with a 10 × handlens by the a) small size, 1–2 mm wide × 0.5–1 cm long, b) tendency to grow in pure dense patches, c) color opaque dark to bright green, and d) leaves near the stem apex crowded and wavy, giving a crisped appearance to the shoot. Also look for a) leaves with 2–5 asymmetric acute to apiculate lobes, b) median leaf cells nearly isodiametric, 30–35 µm wide × 30–40 µm long, the cells relatively thin-walled and without trigones, c) leaf margins often erose because of the frequent development of pale green, tetrahedral to polyhedral gemmae, d) oil-bodies 20–50 per leaf cell, e) underleaves absent on vegetative stems, f) perianth 5–6 plicate, contracted near the apex to a non-beaked lobulate mouth, the lobes with teeth 1–4 cells long, and g) spores 12–15 µm in diameter.

Separation. This species and both subspecies are not easily confused with other liverworts because of their a) size, b) opaqueness of the shoot, c) dark- to bright-green color, d) tendency to grow in dense patches, e) crisped appearance of shoot apices, f) leaves with 2–5 asymmetric acute to apiculate leaf lobes, g) oil-bodies 20–50 per leaf cell, and h) underleaves absent on vegetative stems.
See *L. incisa* subsp. *opacifolia* for separation from that subspecies.

Illustrations. Damsholt 2002; Paton 1999; Schofield 2002; Schuster 1969; Smith 1990.

Habitat. Usually on moist shaded decaying logs; also shaded seepages of rock outcrops and on peaty soil. Elevation from 60 to 1965 m.

Distribution. Lophozia incisa subsp. *incisa* occurs in Europe, Asia, and North America. Calif. Geographic Regions: **KR**: Del Norte Co. *Doyle 11036* (UC), **NC**: Humboldt Co. *Mauer s.n.* (CHSC 20011).

Lophozia incisa (Schrad.) Dumort. subsp. **opacifolia** (Culm. ex Meyl.) R. M. Schust. and Damsh.

Distinctive features. Because of morphological variability of both subspecies of *L. incisa*, subsp. *opacifolia* often can be separated only with difficulty from subsp. *incisa*. Look for a) opaque shoots usually a bluish-green color, b) leaf lobes broadly triangular, each lobe ending in a short, blunt apical cell, c) perianth mouth entire or with a few scattered teeth, and d) spores 14.5–20 µm in diameter.

Separation. L. incisa subsp. *opacifolia* can be separated from subspecies *incisa* by a) plants bluish-green (vs. plants dark to bright green in subsp. *incisa*), b) leaf lobes broadly triangular, each ending in a blunt apical cell (vs. leaf lobes more narrowly triangular and apiculate), c) perianth mouth entire or sparsely dentate (vs. perianth mouth lobulate with teeth), and d) spores 14.5–20.0 µm in diameter (vs. spores 12–15 µm in diameter). In addition, subsp. *opacifolia* usually occurs at higher elevations (over 2000 m) than does subsp. *incisa* (under 2000 m).

Illustrations. Damsholt 2002; Paton 1999; Schuster 1969; Smith 1990.

Habitat. Shaded moist soil and organic matter of creek banks. Elevation from 2210 to 3460 m.

Distribution. Lophozia incisa subsp. *opacifolia* occurs in Europe, Asia, and North America. Calif. Geographic Regions: **SN**: Inyo Co. *Doyle 8836* (UC).

Lophozia latifolia R. M. Schust.

Distinctive features. These pale green (in shade) to purplish-brown (in sun) dioicous plants are 2.0–2.4 mm wide × 0.5–1.0 cm long. Look for a) gemmae purplish to deep purple and bluntly angular, in small clusters on tips of young leaves, b) leaves as wide as long with median cells 25–30 µm wide × 30–40 µm long, usually brownish walls, and small concave trigones, c) leaf lobes often with a reflexed sinus base and each lobe terminating in a single cell, d) oil-bodies 10–15 per leaf cell, e) underleaves absent, and f) perianths brownish or purplish with crenulate perianth mouths.

Separation. This species can be confused with *L. excisa*. *Lophozia latifolia* can be separated by a) dioicous (vs. paroicous in *L. excisa*, b) leaves usually brownish (vs. leaves usually reddish), and c) gemmae irregularly pyriform (vs. gemmae 3–5 polyhedral).

Illustrations. Schuster 1969.

Habitat. Peaty soil and rocks with moss. Elevation from 1500 to 3200 m.

Distribution. Lophozia latifolia occurs in Europe and North America. Calif. Geographic Regions: **SN**: Tulare Co. *Howell 784* (CAS).

Lophozia longiflora (Nees) Schiffn.

Distincttive features. This dioicous species appears to be restricted to decaying logs and stumps. Shoots are 1–3 mm wide × 1.5–5 cm long, pale green, but becoming reddish-brown to reddish with age and sun-exposure. Look for a) shoot apices usually slightly upturned, b) leaves bilobed about 0.2–0.3 their length, the lobes triangular, with acute apices, c) median leaf cells 20–30 μm wide × 24–35 μm long, with thin-walls and coarsely convex to confluent trigones, d) oil-bodies 5–10 per cell, the oil-bodies with numerous small spherules, e) gemmae green, polymorphic, and angular at the leaf tips, f) underleaves absent, and g) perianths often reddish, plicate above and contracted near the apex to a toothed/ciliate mouth, with teeth 1–4 cells long.

Separation. This species occasionally can be confused with *L. ventricosa*. *Lophozia longiflora* can be separated by the combination of a) coarsely convex to confluent trigones (vs. moderate to large trigones in *L. ventricosa*), b) oil-bodies 5–10 per cell (vs. oil-bodies 6–16 per cell), and c) perianth mouth ciliate/toothed with cells 1–4 cells long (vs. perianth mouth toothed with cells 1–2 cells long).

Illustrations. Damsholt 2002; Paton 1999; Schuster 1969; Smith 1990.

Habitat. Damp decaying logs and stumps along streams, meadows, ponds, and lakes. Elevation from to 1500 to 3000 m.

Distribution. Lophozia longiflora occurs in Europe, Asia, and North America. Calif. Geographic Regions: **KR**: Trinity Co. *Doyle 7539* (UC), **SN**: Plumas Co. *Dillingham 1034* (gemmae and perianths) (CHSC).

Lophozia sudetica (Nees ex Huebener) Grolle

Distinctive features. These polymorphic, deep-green to brownish, dioicous plants are 1.5–2.0 mm wide × 0.5–4.0 cm long. With age and sun-exposure, the stem ventral surface and leaf bases often are reddish. Rhizoids often are reddish at the base, but otherwise hyaline. Look for a) leaves roundish or circular, concave to canaliculate, divided to 0.2 their length into 2 very short, triangular lobes, b) leaf lobes usually incurved and separated by a broad, crescentic sinus, c) median leaf cells 18–20 μm wide × 24–25 μm long, and with thin, usually brownish walls, and small to moderately bulging trigones, d) oil-bodies spherical to elliptical, 6–9 per leaf cell, e) gemmae reddish-brown usually present, and f) perianths plicate above and contracted near the apex to a crenulate to denticulate, non-beaked mouth.

Separation. Lophozia sudetica usually can be separated from other species of the genus by the combination of a) leaves roundish, concave, and with a broad, shallow, crescent-shaped sinus, b) median leaf cells 18–20 μm × 24–25 μm, often with thin brownish walls and distinct to bulging trigones, and c) gemmae rust-brown to reddish-brown. *L. sudetica* and *L. wenzelii* have a similar leaf shape, but can be separated by a) gemmae reddish-brown (vs. gemmae light green in *L. wenzelii*), and b) smaller median leaf cells 18–20 μm × 24–25 μm (vs. median leaf cells 22–28 μm × 24–36 μm).

Illustrations. Damsholt 2002; Paton 1999; Schuster 1969; Smith 1990.

Habitat. On rock, soil and occasionally organic substrates. Elevation from 1000 to 3500 m.

Distribution. Lophozia sudetica occurs in Europe, Asia, and North America. Calif. Geographic Regions: **CR**: Shasta Co. *Doyle 10827* (UC), **SN**: El Dorado Co. *Doyle 11145* (UC).

Lophozia ventricosa (Dicks.) Dumort.

Distinctive features. These green to yellow-green dioicous plants are 1.0–2.2 mm wide × 1.0–2.5 cm long. Stems and leaf bases occasionally are reddish in sunny habitats. Look for a) leaves divided to 0.3 their length into 2 subequal lobes with somewhat acute apices, b) median leaf cells thin-walled, 20–30 μm wide × 22–38 μm long with distinct, but never bulging trigones, c) leaves generally 0.9–1.3 times as long as wide, d) gemmae green, and e) oil-bodies usually 6–16 per cell, each oil-body consisting of several minute spherules.

Separation. Thalli of *L. ventricosa* are morphologically variable. See *L. wenzelii* for separation from that species. See *L. excise* for separation from that species.

Illustrations. Damsholt 2002; Paton 1999; Schofield 2002; Schuster 1969; Smith 1990.

Habitat. On soil, rocks and decaying wood of stream banks and rock overhangs. Elevation from 1300 to 3600 m.

Distribution. Lophozia ventricosa occurs in Europe, Asia, and North America. Calif. Geographic Regions: **SN**: El Dorado Co. *Whittemore 4004* (CAS).

Lophozia wenzelii (Nees) Steph.

Distinctive features. Shoots of this dioicous, light- to yellow-green species, often tinged brownish to reddish-brown, are 1.2–2.0 mm wide × 1.0–5.5 cm long. Look for a) broad, concave leaves bilobed up to 0.2 their length, b) leaf lobes usually incurved, especially near the shoot apex, and the sinus often is shallow and crescentic, c) median leaf cells thin-walled 22–28 µm wide × 24–36 µm long, usually with small to moderate concave-sided trigones, d) oil-bodies spherical to ellipsoidal, mostly 4–10 per leaf cell, e) gemmae light green (rarely pinkish), quadrate to weakly polygonal, and f) perianths plicate, contracted near the apex to a lobulate, denticulate mouth.

Separation. Thalli of both *L. wenzelii* and *L. ventricosa* are morphologically variable and both have yellow-green gemmae; the two species occasionally can be difficult to separate. *L. wenzelii* usually can be separated by broadly orbicular, saucer-shaped leaves with incurved lateral margins and leaf lobes (vs. absence of clearly concave leaves with incurved margins and lobes in *L. ventricosa*). *Lophozia wenzelii* and *L. sudetica* have similar leaf shape; see that species for Separation

Illustrations. Damsholt 2002; Paton 1999; Schuster 1969; Smith 1990.

Habitat. Usually exposed wet to boggy habitats; along mountain streams and streamlets in meadows. Elevation from 1100 to 3550 m.

Distribution. Lophozia wenzelii occurs in Europe, Asia, and North America. Calif. Geographic Regions: **CR**: Lassen Co. *Doyle 9802* (UC).

Marsupella Dumort. 1822
(Gymnomitriaceae)

This genus is distinguished by a) transversely inserted leaves in two rows b) leaves usually spreading away from stem—the stem is visible, c) cells of leaf margin living at leaf maturity, d) leaves bilobed up to 1/5 their length, the lobe margins smooth, e) leaf cells often with 2–3 large oil-bodies, f) perianths with a crenulate mouth and shorter than the surrounding female bracts, g) a sporophyte that develops within an erect tubular perigynium, and h) spores mostly 7–13 µm.

Marsupella can be confused with *Gymnomitrion*, from which it can be separated by a) marginal cells of mature leaves living (vs. marginal cells of mature leaves usually dead and whitish), and b) perianth short, but present (vs. perianth lacking or vestigial).

Five species reported in California.

Species Key

1. Leaves bilobed to 0.25 their length with the leaf sinus usually rounded to crescentic; leaf lobes obtuse to slightly pointed; dorsal leaf margins often recurved. . . . . **M. emarginata**
1. Leaves bilobed 0.25 to 0.5 their length with the leaf sinus acute to right angled; leaf lobes acute to broadly rounded; dorsal leaf margins not recurved. . . . . **2.**
2. Trigones in the leaf cells very small or absent. . . . . **M. bolanderi**
2. Trigones in the leaf cells distinct to bulging. . . . . **3.**
3. Leaf lobes broadly rounded to obtuse; dioicous. . . . . **M. sphacelata**
3. Leaf lobes acute; paroicous. . . . . **4.**
4. Plants small, less than 0.4 mm wide; leaf lobes erect. **M. sprucei**
4. Plants larger, 0.4–1.5 mm wide; leaf lobes somewhat lax. . . . . **M. sparsifolia**

Marsupella bolanderi (Austin) Underw.

Distinctive features. This small dioicous species is up to 0.2 mm wide and generally less than 6 mm long. Look for a) shoots reddish-green, reddish-brown or reddish-black, b) leaves bilobed up to 0.3 their length, the lobes acute to obtuse, c) leaf cell walls usually reddish or vinaceous, d) median leaf

cells 16–36 μm, with thin to thick walls and no or small trigones, e) cells of leaf margins 14–25 μm wide, margins often crenulate because of slightly bulging outer walls, and f) female bracts usually bordered with radially elongate marginal cells.

Separation. This species can be confused with small forms of *M. emarginata*. It can be separated by leaf cell walls with no or small trigones (vs. leaf cell walls with conspicuous large trigones in *M. emarginata*).

Illustrations. Frye and Clark 1943; Howe 1899.

Habitat. Moist shaded soil and surface of sandstone boulders, open areas, and under shrubs and trees on hillsides. Elevation from 65 to 850 m.

Distribution. Marsupella bolanderi is endemic to the western United States, from Washington to California. Calif. Geographic Regions: **CC**: Monterey Co. *Doyle 8114* (perianths) (UC), **CR**: Shasta Co. *Kellman 2799* (CAS), **KR**: Siskiyou Co. *Howell 458* (CAS), **NC**: Mendocino Co. *Doyle 10419* (UC), **SC**: Santa Barbara Co.: *Doyle 4196* (perianths) (UC).

Marsupella emarginata (Ehrh.) Dumort.

Distinctive features. This dioicous species usually occurs in dull green, brown, reddish-brown, or blackish patches. Shoots usually are 0.5–2.5 mm wide × 1.0–5.0 cm long. Look for a) dorsal leaf margins reflexed toward the base, b) leaves bilobed to 0.25 their length, with open sinuses, c) leaf lobes triangular, clearly wider than long, d) leaf lobe apices obtuse to slightly pointed, usually standing somewhat stiffly away from the stem, e) median leaf cells 13–25 μm wide, with slightly thickened walls and bulging, often confluent trigones, and f) marginal leaf cells 13–20 μm wide.

Separation. This species and *M. sphacelata* exhibit great morphological variation and often can be difficult to separate. *Marsupella emarginata* usually can be separated by a) leaves bilobed 0.2–0.25 their length (vs. leaves bilobed 0.3–0.6 their length in *M. sphacelata*, b) leaf dorsal margins reflexed toward the base (vs. leaf margins not recurved toward the base), c) leaf lobes clearly wider than long (vs. leaf lobes as long as or longer than wide), d) leaf lobes broadly triangular (vs. leaf lobes usually broadly rounded), and e) sinuses open (vs. sinuses acute and often nearly closed at the base). Perianth details are not helpful in separation of these two species. See *M. bolanderi* for separation from small shoots of *M. emarginata*.

Illustrations. Damsholt 2002; Paton 1999; Schofield 2002; Schuster 1974; Smith 1990.

Habitat. On shaded, damp soil and rock of river banks, ravines and cliffs; occasionally on submerged rocks in creeks. Elevation from 200 to 2700 m.

Distribution. Marsupella emarginata occurs in Europe, Asia. and North America. Calif. Geographic Regions: **CC**: San Mateo Co. *Mueller 6895* (ABSH), **KR**: Del Norte Co. *Doyle 11029* (UC), **NC**: Humboldt Co. *Doyle 2188* (UC), **SN**: Fresno Co. *Shevock 22862* (CAS).

Marsupella sparsifolia (Lindb.) Dumort.

Distinctive features. These paroicous, brownish-green to purplish-black plants are 0.4–1.5 mm wide × 3 cm long. Look for a) leaves transversely inserted and somewhat distant on older stem areas, b) leaves bilobed to 0.25–3.5 their length, with open sinuses, c) leaf lobes broadly ovate to acute, d) median leaf cells 15–24 μm wide × 18–24 μm long, with large bulging trigones, d) marginal leaf cells 12–15 μm wide, and e) perianths with subtending antheridial bracts.

Separation. This paroicous species should not be confused with other California species of the genus.

Illustrations. Damsholt 2002; Paton 1999; Schuster 1974; Smith 1990.

Habitat. On damp to wet soil and rocks near streams and seepages in late snowmelt areas. Elevation above 2000 m.

Distribution. Marsupella sparsifolia occurs in Europe, Asia, South Africa, New Zealand, and North America. Calif. Geographic Regions: **SN**: Madera Co. *Howell 570* (as *M. sphacelata*) (TENN) (reported by Hong 1982; this specimen has not been examined).

Marsupella sphacelata (Gieseke ex Lindenb.) Dumort.

Distinctive features. Terrestrial populations are rigid, blackish-brown, and densely-leaved with leaf lobes tightly overlapping (the stem is not visible). Aquatic populations are lax, dull green to brownish, with leaves somewhat distantly spaced on the stem (the stem is visible). Look for a) leaves bilobed 0.25–0.6 their length, sinuses acute and often closed at the base, and with flat (not recurved) basal margins, b) leaf lobes as long as or longer than wide with broadly rounded apices, and c) median leaf cells 15–25 μm wide × 20–31 μm long, with distinct trigones.

Separation. See *M. emarginata* for separation from that species.

Illustrations. Damsholt 2002; Paton 1999; Schuster 1974; Smith 1990.

Habitat. Higher elevations; damp soil and rocks of creek and lake banks, and drainage channels where it often is periodically submerged in flowing water. Elevation from 1210 to 3600 m.

Distribution. *Marsupella sphacelata* occurs in Europe, Asia, and North America. Calif. Geographic Regions: **CR**: Lassen Co.: *Doyle 6778* (UC), **KR**: Trinity Co. *Doyle 9351* (UC), **SN**: El Dorado Co. *Doyle 8797* (UC).

Marsupella sprucei (Limpr.) Bernet

Distinctive features. These easily overlooked small paroicous plants are 0.2–0.4 mm wide × 0.2–0.5 cm long. Shoots occur in small, dense, dark green, brownish to blackish populations, usually arising from stoloniferous branches. Look for a) leaves bilobed 0.25–0.35 their length with acute to rectangular sinuses, b) leaf margins flat (not reflexed) toward the base, c) leaf lobes triangular with apices acute to obtuse and often ending in 2 superposed cells, d) marginal leaf cells 8–18 μm wide, e) median leaf cells 12–18 μm wide × 15–26 μm long, with slightly thickened walls and mostly bulging trigones.

Separation. This small paroicous species is not easily confused with other California species of the genus.

Illustrations. Damsholt 2002; Paton 1999; Schuster 1974; Smith 1990.

Habitat. Soil on and around rocks of higher elevations. Elevation above 1750 m.

Distribution. *Marsupella sprucei* occurs in Europe, Asia, and North America. Calif. Geographic Regions: **CR**: Shasta Co. *Showers 2613B* (SFSU) (reported by Hong 1982; this specimen was not available for examination).

Mylia Gray 1821
(Jungermanniaceae)

Plants of this dioicous genus usually occur in green to brown mats. Look for a) succubous leaves with thin walls and large, bulging trigones. b) underleaves always present, and c) rhizoids often in dense tufts, especially from leaf and underleaf bases.

One species in California.

Mylia anomala (Hook.) Gray

Distinctive features. These are relatively large dioicous plants with shoots 2.5–3.0 mm wide. Look for a) succubous leaves with large median leaf cells 45–50 μm wide × 50–60 μm long, b) leaf cells thin-walled with large bulging trigones, c) oil-bodies 5–18 per mid-leaf cell, d) underleaves subulate to lanceolate (often obscured by dense rhizoid growth), e) rhizoid development mostly confined to underleaf and leaf bases, f) gemmae green, 2-celled, on the margins of lanceolate leaves, and g) perianths laterally compressed with a smooth to crenulate mouth.

Separation. With the combination of a) large size, b) large median leaf cells with large and bulging trigones, c) underleaves present, and d) laterally compressed perianths, *M. anomala* should not be confused with other California liverworts.

Illustrations. Damsholt 2002; Paton 1999; Schuster 1969; Smith 1990.

Habitat. Coastal; usually associated with *Sphagnum*. Elevation from near sea-level to 260 m.

Distribution. Mylia anomala occurs in Europe, Asia, and North America. Calif. Geographic Regions: **NC**: Humboldt Co. *Doyle 1332* (UC).

Nardia Gray 1821
(Jungermanniaceae)

Species of *Nardia* often occur in green to yellow-brown to reddish-brown patches. Leaf apices are rounded, emarginate or bilobed. Look for a) underleaves present, but often obscured by dense rhizoid growth or are small or ephemeral (search near shoot apices for underleaves), b) numerous rhizoids developing from both stem and leaf bases, and c) perianths shorter than and obscured by the female bracts.

Nardia can be confused with *Jungermannia* when the underleaves are missed. In *Jungermannia*, look for perianths short or long emergent beyond the female bracts (vs. perianths not emergent in *Nardia*).

Two species in California.

Species Key

1. Leaves on vegetative shoots entire to emarginate. . . . . **N. geoscyphus**
1. Leaves on vegetative shoots distinctly bilobed. . . . . **N. insecta**

Excluded. Nardia scalaris (Schrad.) Gray. Based on *Howell 388* (CAS), Sutliffe (1947) reported this species from Big Lagoon, Humboldt Co. However, *Howell 388* was mis-identified: it is *Gyrothyra underwoodiana*. No herbarium specimens of *N. scalaris* were found during this study. This species could not be confirmed for California.

Nardia geoscyphus (De Not.) Lindb.

Distinctive features. These paroicous plants are 0.8–1.5 mm wide and usually occur in somewhat opaque green, brown or reddish-brown patches. Look for a) leaves circular to reniform with rounded to emarginate apices (**note:** leaves on reproductive regions of the shoots are bilobed 0.1–0.2 their length, b) underleaves small, lanceolate to triangular, usually found near the stem apex, c) rhizoids hyaline, brownish or reddish, and d) oil-bodies grayish, granular, 2–3 per leaf cell.

Separation. Both *N. geoscyphus* and *N. insecta* are paroicous, have grayish granular oil-bodies, and have green to reddish to brownish coloration. *Nardia geoscyphus* can be separated by leaf apices rounded or emarginate on non-reproductive stem regions, and shallowly bilobed only on reproductive stem regions (vs. leaf apices uniformly bilobed 0.25–0.5 their length on both vegetative and reproductive regions of the stem in *N. insecta*).

Illustrations. Damsholt 2002; Paton 1999; Schuster 1969; Smith 1990.

Habitat. On mineral soil of creek banks and drainages, and peaty soil of higher elevations. Elevation from 1400 to 2000 m.

Distribution. Nardia geoscyphus occurs in Europe, Asia, and North America. Calif. Geographic Regions: **SN**: Tuolumne Co. *Doyle 11213* (UC).

Nardia insecta Lindb.

Distinctive features. This paroicous species usually occurs in grayish-green to reddish-brown patches. Look for a) leaves uniformly and deeply bilobed 0.25–0.5 their length on both vegetative and reproductive stem regions; b) leaf cells thin-walled, usually with bulging trigones, c) underleaves distinct, lanceolate to triangular and usually at nearly right angles to the stem (and often more easily seen when stems are viewed from the side with the compound microscope), d) rhizoids hyaline to reddish, and d) oil-bodies grayish, granular, 2–3 (up to 5) per leaf cell.

Separation. See *N. geoscyphus* for separation from that species.

Illustrations. Damsholt 2002; Paton 1999; Schuster 1969; Smith 1990.

Habitat. On soil of creek banks and drainages. Elevation 775 to 2000 m.

Distribution. Nardia insecta occurs in Europe and North America. Calif. Geographic Regions: **CR**: Shasta Co. *Showers 3693* (SFSU), **SN**: Alpine Co. *Doyle 10803* (UC).

Plagiochila (Dumort.) Dumort. 1835
(Plagiochilaceae)

This is a genus of large, usually deep green, dioicous plants with succubous, obliquely inserted and long decurrent leaves. The adaxial leaf surface is concave near the leaf base and the dorsal leaf margin often is recurved. Gemmae are lacking and rhizoids generally are absent. Small inconspicuous underleaves usually are visible near the shoot apex.

A single species in California.

Plagiochila porelloides (Torr. ex Nees) Lindenb.

Plagiochila porelloides is a morphologically diverse species. Earlier, this species often was considered to be either a synonym (Howe 1899; Frye and Clark 1945), or a subspecies of *P. asplenioides* (Schuster 1980). Hong (1992) reported both *P. porelloides* and *P. satoi* S. Hatt. for California. However, *P. satoi* now is considered to be a synonym of the morphologically variable *P. porelloides* (So and Grolle 2000).

Distinctive features. These are rather large, green to dark green plants 2.0–5.6 mm wide × 1.5–7.0 cm long. Look for a) leaves ovate with the dorsal margin usually entire, recurved and markedly decurrent, b) ventral leaf margins usually dentate (but occasionally entire) with teeth usually 1–2 cells long and 1–2 cells wide at their base, and c) perianths laterally compressed and elongate with a smooth to ciliate-dentate mouth.

Separation. This distinctive plant is not easily confused with other species of leafy liverworts.

Illustrations. Damsholt 2002; Schofield 2002; Schuster 1980.

Habitat. Soil and rock faces of cliffs; damp soil of banks; decayed logs; trunks of trees; occasionally in seepages and periodically submerged at edges of creeks. Elevation from 50 to 1800 m.

Distribution. Plagiochila porelloides occurs in Europe and North America. Calif. Geographic Regions: **KR**: Del Norte Co. *Doyle 7725* (UC), **NC**: Humboldt Co. *Norris 22359* (UC), **SC**: Los Angeles Co. *Kingman 808* (ABSH).

Pleurocladula Grolle 1979
(Cephaloziaceae)

Species of this genus have a) epidermal cells large, thin-walled and colorless (hyalodermis) surrounding smaller interior cells viewed in stem cross-section, b) bifid leaves nearly transversely inserted, and c) large underleaves often only slightly smaller than the leaves. The presence of distinct underleaves easily separates this genus from somewhat similar appearing species of *Cephalozia* (e.g., *C. pleniceps*).

Excluded. Pleurocladula albescens (Hook.) Grolle. Based on *Howell 510* and *Howell 515*, Sutliffe (1941) reported this species from California. During this study, examination of *Howell 515* (CAS), from Ouzel Creek, Tulare Co., Sierra Nevada, found only *Anthelia juratzkana* and very poorly preserved plants of *Lophozia* sp.; no plants with a hyalodermis or distinct underleaves were found. Unfortunately, *Howell 510*, from Reflection Lake, Tulare Co., Sierra Nevada, was not located. Hong (1988b) reported *P. albescens* from California, but no collection was cited and he did not enter it on his distribution map. *Pleurocladula albescens* occurs in Europe, Asia, and North America. It is rare in Oregon. Although this genus could not be confirmed for California, the above description of the genus should aid in its identification. Look for it in margins of wet meadows, seepages and drainages in Arctic/Alpine elevations. See Damsholt (2002), Paton (1999), or Schofield (2002) for Illustrations

Porella L. 1753
(Porellaceae)

Once seen, this distinctive genus is easily recognized in the field. Plants usually grow as large mats on tree trunks and shaded rock outcrops, less commonly on soil. Look for a) leaves complicate-bilobed with incubous dorsal lobes, b) ventral lobes much smaller than the dorsal, but never forming water-sacs as in *Frullania*, c) underleaves not lobed, and d) perianths mostly dorsiventrally flattened, especially above the middle.

The genus is dioicous and male and female plants usually occur in separate mats. Search carefully for both female plants with perianths and male plants with antheridial branches. Not only are details of the perianth mouth helpful in species identification, but collection of both female and male plants result in complete species documentation.

Although the genus is easy to identify, species determination of vegetative plants can be difficult because of morphological variability. There are two iodine tests that can be used to separate the polymorphic *P. cordaeana* from the other California species of the genus. (1) Piippo and Norris (1996) described the use of iodine potassium-iodide, IKI. (IKI might be obtained from the Botany or Biology Department of a nearby university or college. **USE WITH CARE—IKI IS A POISON**). (2) David Wagner (personal communication) recommended the use of emergency drinking water germicidal tablets (e.g., Coghlan's or Potable Agua). A concentrated solution (2–3 tablets dissolved in 10 cc of water) works quickly and uniformly. A neutralizing agent can be purchased with Potable Agua.

For examination, remove with tweezers one or two (fresh or dry) mature leaves from a stem and put the leaves in a small drop of IKI or germicidal solution on a microscope slide. Leaves of *P. cordaeana* quickly darken and become nearly black as observed with the high power of the dissection microscope. Add a coverslip for a detailed examination of leaf cell contents under the compound microscope. A region of the leaf cells of *P. cordaeana* will have a violet coloration with IKI or a bluish coloration with the germicidal tablet solution. Leaf cell contents of the other California species lack this violet or blue coloration.

The intensity of the coloration is variable, apparently depending upon the physiological condition of the plant at the time of collection, rather than the age of the herbarium specimen. For example, *Howe s.n.* (May 7, 1892) (ABSH) of *P. cordaeana* from Marin County still gave an intense violet color reaction with IKI. Cells of young leaves near the shoot apex often stain less intensely, and some not at all.

Four species in California.

Species Key

In the following key, start at 1. when IKI or germicidal solution is used; start at 2. when not used.

1. Leaf cell contents darken and have a violet or blue coloration. . . . . **P. cordaeana**
1. Leaf cell contents do not darken and do not have a violet or blue coloration. . . . . **2.**
2. Cells of mature leaves with large and bulging trigones; underleaves about the same width as the ventral lobes; perianth mouth wide and usually entire when mature, but short-ciliated or toothed when young; perianth apex usually transversely recurved, giving the perianth a truncated appearance. . . . . **P. navicularis**
2. Cells of mature leaves with minute, small or moderate trigones; underleaves only slightly to much wider than ventral lobes; perianth mouth wide and coarsely dentate, or narrow and smooth or ciliated; perianth apex obliquely or not recurved. . . . . **3.**
3. Ventral lobes not or only short decurrent; perianth mouth wide and coarsely toothed; taste peppery in fresh material. . . . . **P. roellii**
3. Ventral lobes long-decurrent; perianth mouth narrow and smooth or ciliated; taste aromatic, not peppery, in fresh material. . . . . **4.**
4. Underleaves on mature stems usually distant, apices rounded; cells of dorsal lobes with small to medium trigones; perianth mouth usually smooth. . . . . **P. cordaeana**
4. Underleaves on mature stems usually overlapping, apices acute; cells of dorsal lobes usually with minute trigones; perianth mouth ciliated. . . . . **P. bolanderi**

Excluded. Porella platyphylla (L.) Pfeiff. The reports by Clark and Frye (1936), Frye and Clark (1946) and Hong (1983) of this species in California were based on the *Frye 2121*, March 27, 1934 collection from a rock wall in a gorge near Salyer, Trinity County (WTU). In the WTU specimen packet, David Wagner had placed an annotation label, dated April 1990, with the corrected identification of *P. roellii* Steph. *Frye 2121* was examined during this study and was found to have perianths typical of *P. roellii*, confirming Wagner's identification. Moreover, all herbarium specimens from California that had been labeled *P. platyphylla* and examined in this study were mis-identified. *Porella platyphylla* could not be confirmed for California.

Porella bolanderi (Austin) Pearson

Distinctive features. This species is most easily identified by perianth characteristics. Look for a) perianth ventral surface weakly to strongly 2–5 plicate, b) perianth usually narrowed at the apex to

0.3 or less of the width of the perianth, and c) a ciliate perianth mouth with uniseriate filaments 2–6 cells in length.

Vegetative plants are variable in morphology. The plants are irregularly branched, once to twice pinnate, with shoots 2–4 mm wide and up to 6 cm long. The dorsal lobes are dark to olive-green and not glossy. In drier habitats, the dorsal lobes are closely to tightly imbricate, and the margins often are slightly upturned. In more humid habitats and young plants, the lobes are more remote and flat. Margins of the dorsal lobes of plants from drier habitats often have several rows of dead, colorless cells, which contrast sharply with the living cells. Look for a) one or more teeth often on the basal margin of the dorsal lobe, b) underleaves long decurrent and, on mature branches, usually overlapping, c) underleaf tip recurved and usually acute, and d) underleaf margins toothed to laciniate toward the base.

Caution. The plants often occur in large mats. Growing through the mats usually are narrower shoots that have dorsal, ventral and underleaf morphologies similar to those of *P. cordaeana*. However, these shoots usually can be traced back as branches from mature stems of *P. bolanderi*. Occasionally, some of the first–formed underleaves on these narrow shoots have bifid tips, mimicking the underleaves of *Frullania*.

Separation. New growth, young plants, plants growing in humid or wet habitats, and narrow branches growing through mats can be confused with the highly polymorphic *P. cordaeana*. The IKI or germicidal solution test is the quickest and most accurate method to separate these two species; the cell contents of *P. bolanderi* do not react with IKI or germicidal solution (vs. appearance of a violet or blue color in *P. cordaeana*). *Porella bolanderi* also can be separated by the a) perianth distinctly plicate, especially ventrally (vs. perianth not plicate in *P. cordaeana*) and b) perianth mouth ciliate (vs. perianth mouth smooth or toothed).

Illustrations. Frye and Clark 1946; Howe 1899, Piippo and Norris 1996.

Habitat. On trunks of angiosperms, shaded boulders and rock outcrops; occasionally on shaded soil of canyon walls. Elevation from near sea-level to 1500 m, but mostly below 800 m.

Distribution. Porella bolanderi is endemic to western North America. Calif. Geographic Regions: **CC**: Contra Costa Co. *Shevock 24516* (CAS), **CR**: Shasta Co. *Doyle 2904* (UC), **NC**: Humboldt Co. *Norris 84073* (UC), **SC**: Ventura Co. *Sagar 957* (SFV), **SN**: Tulare Co. *Doyle 6977* (UC).

Porella cordaeana (Huebener) Moore

Distinctive characteristics. This species is irregularly 1–2 pinnate, with the side branches narrower than the main branch; the main branches are 2.5–4.0 mm wide and up to 10 cm long. This is a highly polymorphic species. In wet or humid habitats, the plants usually are dark-green and not, or only a little, glossy; in drier or more exposed habitats, the plants usually are olive- to brownish-green to green, and somewhat glossy. The form of the ventral lobes and underleaves also is variable in different habitats. First, look for a positive response to IKI or germicidal solution. Also look for a) underleaves long decurrent with rounded apices, and not or only little overlapping on mature parts of main branches (however, on young or rapidly growing branches, the underleaves often overlap and the apices are somewhat acute), b) a perianth smooth, not plicate (occasionally there is a single central low longitudinal fold on the ventral surface of young perianths, which disappears with sporophyte development), c) a perianth that usually is obliquely recurved from below the middle to the apex, and d) a narrow perianth mouth less than 0.3 the width of the perianth, generally smooth, but occasionally sinuate with teeth on the sinuations.

Separation. Porella cordaeana can be difficult to separate from *P. bolanderi*, because of the morphological variability of the vegetative shoots of these two species. A positive IKI or germicidal solution test most easily separates *P. cordaeana* from *P. bolanderi* (and from other California species of *Porella*). In the absence of IKI or germicidal solution, see *P. bolanderi* for separation of that species.

Illustrations. Frye and Clark 1946; Piippo and Norris 1996.

Habitat. Both dry and humid environments; on boulders, rock outcrops and tree trunks; rarely on soil. Elevation from near sea-level to 2750 m, but more common below 2000 m.

Distribution. Porella cordaeana occurs in Europe, Asia, and North Africa, and apparently is restricted to the western part of North America. Calif. Geographic Regions: **CC**: Monterey Co. *Doyle 10894* (UC), **CR**: Tehama Co. *Doyle 8632* (UC), **KR** Siskiyou Co. *Lenz 1059* (UC), **MP**: Modoc Co.

Doyle 6688 (UC), **NC** Marin Co. *Howe s.n.* (May 7, 1892) (ABSH), **SC**: Los Angeles Co. *Smith 2* (CHSC), **SN**: Amador Co. *Norris 82870* (UC).

Porella navicularis (Lehm. and Lindenb.) Lindb.

Distinctive features. These are rather shiny, dark green, yellowish-brown or yellowish-green plants that usually occur in large mats. The shoots are more-or-less regularly bipinnate; the main branches 2.5–4.5 mm wide and up to 12 cm long. Look for a) median cells of the dorsal and ventral lobes (and cells of underleaves and perianths) with large bulging trigones on mature parts of the shoots, b) ventral lobes and underleaves of similar size, c) on female plants, a few small leaves on the short stem between the main branch and the perianth, d) a perianth flattened and non-plicate, only slightly narrowed at the apex, usually transversely recurved near the apex, giving the perianth a truncate appearance, e) a wide perianth mouth that usually is entire when mature, but often short-ciliate or toothed when young.

Separation. With a) large, bulging trigones in cells of the dorsal and ventral lobes, underleaves, and perianths, b) underleaves and ventral lobes of nearly the same width, and c) perianth apex recurved, *P. navicularis* is not easily confused with other California species of *Porella*.

Illustrations. Frye and Clark 1946; Howe 1899, Piippo and Norris 1996; Schofield 2002.

Habitat. Commonly on trunks and branches of angiosperms, especially *Quercus*; also on logs and rocks; less commonly on conifers. Elevation from near sea-level to 2400 m, but most often below 800 m.

Distribution. Porella navicularis is endemic to western North America and is especially common along the Pacific Coast from southeast Alaska to California. Calif. Geographic Regions: **CC**: San Mateo Co. *Doyle 10377* (UC), **KR**: Siskiyou Co. *Norris 67798* (UC), **NC**: Mendocino Co. *Doyle 9068* (UC).

Porella roellii Steph.

Distinctive features. The distinctive peppery taste of living plants is the easiest way to identify this species in the field. These are shiny, dark green to yellowish-brown plants. The shoots are 1–2 times pinnately branched; main branches are 1.5–2.2 mm wide and up to 8 cm long. Plants with perianths are easily identified. Look for a) a non-plicate perianth only occasionally slightly obliquely recurved, b) a perianth mouth wide (but usually slightly contracted), sinuate, with coarse teeth (1–4 cells long and 1–4 cells wide at the base) on the sinuations, and c) leaves 2–6 on the short stem between the perianth and the main branch.

On vegetative plants, look for a) trigones small to medium (occasionally large in very old leaf cells) in cells of the dorsal leaf lobe, and b) ventral lobes more-or-less parallel to the stem, especially on young branches, generally narrower than the underleaves, and not, or only little, decurrent, narrowed to an often obtuse or acute apex, and broadly rounded or with a blunt spur at the base.

Separation. The peppery taste is the easiest field-test to separate this plant from the other California species of the genus. Vegetative plants of herbarium specimens can be confused with *P. cordaeana*, but can be separated by a) lack of a violet or blue reaction with IKI or germicidal solution (vs. a violet or blue reaction in *P. cordaeana*), b) the ventral lobe little decurrent (vs. ventral lobe long decurrent), c) underleaves on mature stems clearly overlap (vs. underleaves on mature stems with little or no overlap), d) short branch between the perianth and the main branch with 2–6 normal leaves (vs. normal leaves on the short branch absent), and e) a perianth with a wide mouth (vs. a perianth narrowed toward the apex, with a narrow mouth).

Shoots of both *P. roellii* and *P. navicularis* have a shiny appearance and can be of similar color. However, *P. roellii* has a) mature leaf cells without large bulging trigones (vs. mature leaf cells with large bulging trigones in *P. navicularis*) and b) perianth apex only occasionally obliquely recurved (vs. perianth apex usually transversely recurved).

Illustrations. Frye and Clark 1946; Howe 1899, Piippo and Norris 1996.

Habitat. On rocks, boulders and tree trunks (especially angiosperms); less often on logs and soil; usually occurs in humid habitats, e.g., near streams in canyon bottoms and outcrops in narrow ravines. Elevation from near sea-level to 1800 m; more common below 1200 m.

Distribution. Porella roellii is restricted to western North America, from Alaska to California. Calif. Geographic Regions: **CC**: Monterey Co. *Doyle 8886* (UC), **KR**: Trinity Co. *Doyle 7532* (UC), **NC**: Sonoma Co. *Mason 2519* (perianths) (UC); **SN**: Plumas Co. *Norris 52647* (UC).

Ptilidium Nees 1833
(Ptilidiaceae)

Plants of this brownish to reddish-brown genus occur in large or small patches. The incubous leaves are deeply bilobed, with each lobe divided 1–3 times. Slender cilia occur at the lobe tips and margins. The large underleaves also are bilobed and have ciliate margins.

One species in California.

Ptilidium californicum (Austin) Pearson

Distinctive features. These yellowish-brown to reddish-brown plants often grow in dense mats, but easily can be overlooked when small populations grow intermixed with moss. Look for a) leaves 3–4 lobed with filamentous lobe apices and margins, decurrent on the dorsal stem surface, b) leaf cells medium-thick to thick-walled with bulging trigones, c) underleaves about 0.5 the size of the leaves, with ciliate margins, and d) perianths plicate and narrowed to a ciliate mouth.

Separation. A very distinctive plant; when once seen it is difficult to confuse with any other California liverwort.

Illustrations. Frye and Clark 1943; Howe 1899; Schofield 2002.

Habitat. Usually on trunks of *Abies concolor, A. magnifica*, and *Pseudotsuga menziesii*; less frequently on snags and decaying conifer logs. Elevation from 420 to 1878 m.

Distribution. Ptilidium californicum is endemic to coastal western North America, from Alaska to California. Calif. Geographic Regions: **CR**: Shasta Co. *Williams 72799b* (UC), **KR**: Siskiyou Co. *Ziegler JRZ005* (UC), **NC**: Humboldt Co. *Norris 57738* (NY).

Radula Dumort. 1833
(Radulaceae)

Plants of this genus have complicate-bilobed leaves with the dorsal lobe larger than the ventral lobe. Look for a) ventral lobes usually flattened and appressed to the dorsal lobe, b) underleaves absent, c) oil-bodies large, brownish, plate-like, 1 (occasionally to 3) per dorsal lobe cell, d) rhizoids restricted to a small area at the base of the ventral leaf lobe, and e) truncate perianth mouth.

Radula is similar to *Frullania* and *Porella* in its complicate-bilobed leaves with the dorsal lobe larger than the ventral lobe. It is easily separated from both genera by a) underleaves absent, b) rhizoids developing at the base of the ventral lobe, and c) oil-bodies large, plate-like, usually only 1 per mature dorsal lobe cell.

Two species in California.

Species Key

1. Dorsal lobe inner margin adnate to the stem, the apical region not extending across the stem; cells in the middle of the dorsal lobe 9–18 μm long; gemmae absent; rhizoids scarce to absent; large oil-body nearly filling the cell lumen; dioicous. . . . . **R. bolanderi**
1. Dorsal lobe inner margin not adnate to stem, the apical region usually extending across the stem; cells in the middle of the dorsal lobe 15–30 μm long; gemmae occasionally present on leaf margins; rhizoids abundant; oil-body filling only about 0.5 of cell lumen; monoicous. . . . . **R. complanata**

Radula bolanderi Gottsche

Distinctive features. These dioicous plants usually occur in light- to gray-green patches. Look for a) the dorsal leaf lobe inner margin adnate to the stem, the apical region not extending beyond the stem, b) median dorsal lobe cells 9–18 μm long, c) mature dorsal lobe cells usually with 1 large oil-body nearly filling the cell lumen, d) rhizoids infrequent, e) gemmae absent, f) male plants with conspicuous "catkin-like" antheridial branches, g) female plants with perianths terminal on main branches, and h) spores 38–58 μm in diameter.

Separation. *Radula bolanderi* is readily separated from *R. complanata* by a) the dorsal lobe inner margin adnate to the stem (vs. the dorsal lobe inner margin not adnate to the stem in *R. complanata*), b) a single large oil-body nearly filling the cell lumen (vs. the single oil-body filling about 0.5 the cell lumen), c) rhizoids infrequent (vs. rhizoids abundant), d) gemmae absent (vs. gemmae frequently present), e) dioicous (vs. usually paroicous), and f) spores 38–58 μm (vs. spores 26–40 μm).

Illustrations. Clark and Frye 1928.

Habitat. Most commonly on trunks and branches of angiosperms, but occasionally on young *Pseudotsuga, Sequoia*, and *Calocedrus*; less frequently on soil, logs and boulders. Elevation from 15 to 1200 m; mostly below 400 m.

Distribution. *Radula bolanderi* is endemic to western North America. Calif. Geographic Regions: **CC**: Monterey Co. *Doyle 8919* (UC), **KR**: Trinity Co. *Norris 77258* (UC), **NC**: Marin Co. *Howe 3* (as *R. spicata)* (male and female) (NY).

Radula complanata (L.) Dumort.

Distinctive features. Plants of this paroicous species usually occur in yellowish- to dark-green patches. Look for a) the dorsal lobe inner margin not adnate to the stem, the apical region extending beyond the stem, b) median dorsal lobe cells 15–30 μm long, c) mature dorsal lobe cells with 1 oil-body filling about 0.5 the cell lumen, d) rhizoids frequent, e) gemmae occasionally present on the leaf margins, f) perianths terminal on short or main branches, g) male bracts conspicuous below the perianths, and h) spores 26–40 μm in diameter.

Separation. See *R. bolanderi* for separation from that species.

Illustrations. Frye and Clark 1946; Damsholt 2002; Paton 1999; Schofield 2002; Schuster 1980.

Habitat. Usually on trunks and branches of angiosperms; also on *Taxus* and young *Pseudotsuga*; less commonly on rocks and boulders; Elevation from near sea-level to 1850 m.

Distribution. *Radula complanata* occurs in Europe, Asia, North Africa, and North America. Calif. Geographic Regions: **CC**: San Mateo Co. *Doyle 10388* (UC), **KR**: Siskiyou Co. *Doyle 9272* (gemmae) (UC), **NC**: Humboldt Co. *Norris 56311* (UC), **SC**: Santa Barbara Co. *Norris 102064* (UC), **SN**: Fresno Co. *Shevock 14498* (UC).

Scapania (Dumort.) Dumort. 1835
(Scapaniaceae)

Leaves of this genus are complicate-bilobed with the dorsal lobe slightly or greatly smaller than the ventral lobe. The leaves of most species are keeled at the fold. Look for a) epidermal and subepidermal cells of the stem (usually referred to as cortical cells) pigmented and thick-walled, surrounding thinner-walled medullary cells, b) underleaves absent, c) gemmae ellipsoidal, ovoid or pyriform, 1–2 celled, and d) perianths dorsiventrally flattened with a truncate mouth.

Caution. Several species of this genus exhibit considerable morphological plasticity. In addition, the color, size and form of juvenile plants can differ greatly from mature ones. Healthy, mature, robust parts of plants must be used for identification purposes.

Ten species plus one variety in California.

Species Key

1. Dorsal leaf lobe nearly the same size as the ventral lobe (subequal); both lobes with generally similar orientation to the stem. . . . . **2.**
1. Dorsal leaf lobe clearly smaller than ventral lobe (unequal); dorsal lobe generally more spreading from the stem than the ventral lobe. . . . . **3.**
2. Small plants, 1–2.7 mm wide, 1–2.2 cm long; basal part of leaf more-or-less appressed to and sheathing the stem; leaf margins entire; leaf fold not or scarcely keeled; gemmae generally dark brown to reddish. . . . . **S. cuspiduligera**
2. Larger plants, 2–4.5 mm wide, 1–7 cm long; basal part of leaf not appressed to or sheathing the stem; leaf margins usually finely denticulate; leaf fold weakly to clearly keeled; gemmae green (seldom pink or purplish-red). . . . . **S. subalpina**
3. Ventral leaf lobe not decurrent, or short decurrent to little more than level of attachment of the keel to the stem. . . . . **4.**

3. Ventral leaf lobe long decurrent beyond the level of attachment of the keel. . . . . **7.**
4. Leaves with broad ventral lobes (often nearly as wide as long); ventral lobes abruptly narrowed to the base; plants more than 2 cm in length. **S. irrigua**
4. Leaves with narrow ventral lobes (clearly longer than wide); ventral lobes gradually narrowed to the base; plants small, 2 cm or less in length. . . . . **5.**
5. Leaves usually bordered with 1–4 rows of uniformly thick-walled cells. . . . . **S. curta**
5. Leaf margins with thin-walled cells, or if bordered, then walls not uniformly thickened. . . **6.**
6. Ventral lobe apices usually broadly rounded; perianth mouth entire or with a few, scattered teeth. . . . . **S. scandica**
6. Ventral lobe apices mostly acute and apiculate; perianth mouth laciniate with large, close teeth. . . . . **S. mucronata**
7. Plants small, less than 2.5 mm wide. . . . . **S. umbrosa**
7. Plants large, more than 2.8 mm wide. . . . . **8.**
8. Dorsal lobe margin teeth strongly developed, larger and more widely spaced than those on the ventral lobe; dorsal lobe basal margin usually with branched (often antleroid) cilia. . . . . **S. bolanderi**
8. Dorsal lobe margin either entire or toothed, teeth, when present, generally similar in size and spacing, or smaller and fewer than on the ventral lobe; dorsal lobe basal margin entire, toothed or with unbranched cilia. . . . . **9.**
9. Dorsal lobes clearly decurrent on stem; thick-walled pigmented epidermal cells interrupted on the ventral stem surface by thinner-walled cells viewed in stem cross-section. **S. americana**
9. Dorsal lobes not (or only slightly) decurrent on stem; thick-walled pigmented epidermal cells not interrupted by thinner-walled cells in stem cross-section. . . . . **10.**
10. Leaf margins dentate, with conspicuous teeth on the keel. . . . . **S. undulata** var. **oakesii**
10. Leaf margins entire to dentate, but lacking teeth on the keel. . . . . **S. undulata** var. **undulata**

Excluded. 1) *Scapania evansii* Bryhn. Clark and Frye (1936) reported this species from Califonia, based on a collection by Frye. However, WTU has no California specimen of *S. evansii*. No herbarium specimen of this species was located during this study. *Scapania evansii* could not be confirmed for California.

2) *Scapania glaucocephala* (Taylor) Austin. Based on *Howe 58* (UC) collected in Russian Gulch, Mendocino Co., Howe (1897a) and Hong (1980) reported this species from California. Howe (1899, p. 153–154) later changed his mind and referred to *Howe 58* as "an abortive, gemmiferous condition of *Scapania umbrosa*". In 2000, Alan Whittemore annotated this specimen as "probably depauparate *S. umbrosa*". Examination of *Howe 58* during this study confirmed the determinations by Howe and Whittemore. No herbarium specimens of *S. glaucocephala* from California were located during this study. This species could not be confirmed for California.

3) *Scapania nemorea* (L.) Grolle (= *S. nemorosa* (L.) Dumort). Early bryologists, e.g., Howe (1896), reported *S. nemorea* from California but the western North American plants were shown by Evans (1930) to be *S. americana*. No herbarium specimens of *S. nemorea* from California were located during this study. The species could not be confirmed for California.

Scapania americana Müll. Frib.

Amakawa (1967) has shown that *Scapania granulifera* A. Evans is conspecific with *S. americana*. Specimens examined during this study support that conclusion.

Distinctive features. Plants in green to golden-brown to purplish-red tufts or patches. Look for a) dorsal and ventral lobe margins ciliate or dentate, the dorsal lobe usually with fewer and shorter teeth (1–3 cells long) than the ventral lobe (1–5 cells long), b) dorsal lobes with unbranched teeth at their base, c) dorsal and ventral lobes distinctly decurrent, d) leaf surfaces often roughened with large (granulifera-type) or small wart-like or elongate papillae (the number and size of papillae is variable between and within populations), e) in stem cross-section, a deeply pigmented, thick-walled epidermis interrupted on the ventral side by 2–4 cells with thinner walls and little to no pigmentation f) gemmae 2-celled, golden-brown to reddish, and g) perianth mouth with ciliate lobes.

Separation. This species occasionally can be confused with *S. bolanderi*. See *S. bolanderi* for Separation

Illustrations. Evans 1930.

Habitat. Primarily on soil and rocks of outcrops and banks; seldom on wood. Elevation from 40 to 2275 m, mostly below 1000 m.

Distribution. *Scapania americana* is endemic to western North America. Calif. Geographic Regions: **CC**: San Mateo Co. *Doyle 6065* (perianths) (UC), **KR**: Del Norte Co. *Doyle 9760* (perianths) (UC), **NC**: Marin Co. *Howe 21* (UC), **SN**: Tulare Co.: *Laeger 1936* (CAS).

Scapania bolanderi Austin

Distinctive features. This species grows in large greenish to yellow-green mats or as small shoots with other bryophytes. Look for a) dorsal and ventral lobes coarsely dentate, with teeth forming broad triangles, b) the ventral lobe spreading widely from stem axis, the margins often broadly recurved, with smaller and more frequent teeth than on the dorsal lobe, c) the dorsal lobe base usually with branched, multicellular cilia, resulting in an antleroid appearance, d) the dorsal lobe not or little decurrent, but the ventral lobe clearly decurrent, e) in stem cross-section, a deeply pigmented, thick-walled epidermis interrupted on the ventral side by 2–4 cells with thinner walls and little to no pigmentation, f) gemmae green, and g) perianth mouth coarsely lobed.

Separation. *Scapania bolanderi* and *S. americana* are the only California species with a strip of thinner-walled cells that interrupt the thick-walled epidermis on the ventral side of the stem. *S. bolanderi* can be separated from S. *americana* by: a) leaf teeth that form broad triangles and have blunt apices (vs. leaf teeth elongate triangles with slender apices in *S. americana*); b) dorsal lobes with distinctly fewer and coarser teeth than ventral lobes (vs. dorsal lobes with somewhat similar teeth as on ventral lobes); c) basal portion of dorsal lobe ciliate, the cilia usually branched, antleroid (vs. basal portion of dorsal lobe entire to short-dentate not ciliate or antleroid); and d) green gemmae with hyaline cell walls (vs. gemmae with golden-brown cell walls). In addition, *S. bolanderi* nearly always occurs on organic substrates (but exceptions occur, as in *Doyle 7846* [UC]) (vs. *S. americana* commonly occurring on inorganic substrates).

Illustrations. Evans 1930; Howe 1899; Schofield 2002.

Habitat. Primarily on shaded trunks of hardwoods and softwoods; also on logs, burned stumps, soil and rock outcrops. Elevation from 30 to 3000 m; mostly below 800 m.

Distribution. *Scapania bolanderi* occurs on the Pacific Coast of Asia and North America. Calif. Geographic Regions: **CC**: San Mateo Co, *Doyle 10378* (UC), **KR**: Del Norte Co. *Doyle 10598* (UC), **NC**: Humboldt Co. *Shevock 16728* (CAS), **SN**: Tulare Co.: *Doyle 7846* (UC).

Scapania curta (Mart.) Dumort.

Distinctive features. These small polymorphic plants usually are less than 2.5 mm wide and up to 1.5 cm long. The plants often have a vinaceous ventral surface. Look for a) leaves margined with a border of 1–4 uniformly thick-walled cells, b) median leaf cells thin-walled, 20–23 μm wide × 21–24 μm long, with small trigones, c) ventral lobe apices mostly rounded, margins entire (sometimes with a few 1-celled teeth near the apex), bases often vinaceous; and not, or only little, decurrent, d) dorsal lobe apices not directed toward the shoot apex and not decurrent, e) large dorsal lobe over 0.65 the area of the ventral lobe, f) gemmae greenish, 2-celled, and g) perianth mouth with few scattered 1–2-celled teeth.

Separation. In size and morphological variability, *S. curta* occasionally can be difficult to separate from *S. mucronata* and *S. scandica*. Usually, it can be separated from *S. mucronata* by a) leaves with a border of uniformly thick-walled cells without trigones (vs. leaves not bordered with thick-walled cells without trigones in *S. mucronata*), b) teeth occasionally present near the lobe apices (vs. teeth never present near the the lobe apices), c) shoots often with a reddish coloration, especially in sun forms (vs. shoots often with a brownish coloration, but never reddish), and d) perianth mouth sparsely toothed (vs. perianth mouth laciniate with large close teeth).

Both *S. curta* and *S. scandica* have broadly rounded ventral lobes and a perianth mouth with a few scattered teeth. *Scapania curta* can be separated by a) leaf with a distinct 1–4-celled marginal border of uniformly thick-walled cells (vs. leaf marginal border absent, or, if present, a 1–2-celled border, but not uniformly thick-walled in *S. scandica*), and b) a large dorsal lobe over 0.65 the area of the ventral lobe (vs. a dorsal lobe 0.5–0.65 the area of the ventral lobe).

Illustrations. Damsholt 2002; Paton 1999; Schuster 1974; Smith 1990.

Habitat. On mineral and peaty soil and wood along streams. Elevation from 2050 to 3450 m.

Distribution. Scapania curta occurs in Europe, Asia, and North America. Calif. Geographic Regions: **SN**: Inyo Co. *Doyle 8742* (perianths) (UC).

Scapania cuspiduligera (Nees) Müll. Frib.

Distinctive features. This is a small pale-, whitish-, yellowish-, or brownish-green plant, 1.0–2.7 mm wide × 0.6–2.2 cm long. Look for a) subequally bilobed leaves (the lobes similar in size and shape), smooth margins bordered with 1–3 rows of thick-walled cells, and evenly rounded lobe apices, b) leaf without a sharp keel and with the leaf base sheathing the stem, c) dorsal leaf lobe usually upturned, giving the shoot a crisped appearance, d) leaf cells often with large trigones, e) gemmae frequent, forming dark brown to reddish-brown clusters near the shoot apex, f) ventral leaf lobes clearly decurrent, and g) perianth mouth smooth (rarely with a few teeth).

Separation. This species can resemble small shoots of *S. subalpina*. See that species for separation

Illustrations. Damsholt 2002; Paton 1999; Schuster 1974; Smith 1990.

Habitat. Usually on damp or wet rock and cliff outcrops, mostly on basic substrates. Elevation above 1750 m.

Distribution. Scapania cuspiduligera occurs in Europe, Asia, and North America. Calif. Geographic Regions: **CR**: Shasta Co. *Doyle 9878* (brownish gemmae) (UC), **SN**: Mono Co. *Doyle 9813* (brownish gemmae) (UC).

Scapania irrigua (Nees) Gottsche, Lindenb. and Nees

Distinctive features. This is a moderately-sized yellowish-green to brown plant, up to 4 mm wide. Look for a) ventral lobes broadly reniform to cordate, almost as wide as long, often with acute apices and abruptly narrowed to the base, b) ventral leaf lobes not decurrent or seldom decurrent to below the level of insertion of keel, c) dorsal leaf lobes with a pointed apex and not decurrent, d) cells of leaf margins thin-walled to slightly thickened, the marginal cells not differentiated from the interior cells, e) leaves with smooth margins (but teeth occur near apices with gemmae), f) gemmae green, 2-celled, slender and often in large clusters at the shoot apex, and g) perianth mouth dentate to short ciliate, 1–4 cells long.

Separation. Robust, mature plants should not be confused with other California species of *Scapania*. Look for mature shoots to study because juvenile or poorly developed plants can be mistaken for *S. scandica* or *S. curta*.

Illustrations. Damsholt 2002; Paton 1999; Schuster 1974; Smith 1990.

Habitat. Often around standing or slow flowing water, but rarely submerged; on soil in meadows and on logs; sunny rocky banks of lakes, ponds, bogs, pools, and seepages; Elevation up to 2660 m.

Distribution. Scapania irrigua occurs in Europe, Asia, and North America. Calif. Geographic Regions: **SN**: Nevada Co. *Whittemore 4159* (MO).

Scapania mucronata H. Buch

Distinctive features. These are small green to brown plants, mostly less than 2.5 mm wide. Look for a) marginal cells of both the dorsal and ventral lobes more-or-less isodiametric, 14–20 μm in diameter, b) leaf lobe marginal cells mostly thin-walled, not forming a distinct border, and usually with large bulging trigones, c) ventral lobe apices apiculate, d) leaf margins smooth except near gemmae development, e) oil-bodies present in marginal cells, e) gemmae green to reddish, 2-celled, common, and g) perianth mouth mostly laciniate with tapering teeth (2–5 cells wide at the base and several cells long).

Separation. This species can be confused with *S. curta* and *S. scandica. Scapania mucronata* can be separated from *S. scandica* by a) apiculate ventral lobe apices (vs. ventral lobe apices rounded in *S. scandica*), and b) perianth mouths mostly laciniate with large close teeth (vs. perianth mouth smooth or with a few scattered teeth). See *S. curta* for separation from that species.

Illustrations. Damsholt 2002; Paton 1999; Schuster 1974; Smith 1990.

Habitat. On shaded soil, boulders and rock cliff faces. Elevation above 1000 m.

Distribution. Scapania mucronata occurs in Europe, Asia, and North America. Calif. Geographic Regions: **KR**: Trinity Co. *Doyle 7557* (UC), **MP**: Modoc Co. *Doyle 6670* (gemmae) (UC).

Scapania scandica (Arnell & H. Buch) Macvicar

Distinctive features. This is a small pale green to reddish-brown plant mostly less than 2.5 mm wide and up to 1.5 cm long. Look for a) leaf lobe margins usually entire except when gemmiferous, then with a few scattered spinose teeth near places of gemmae development, b) median leaf cells 16–19 μm wide × 18–24 μm long, c) marginal leaf cell walls usually thin or slightly thickened, with trigones (**note:** the marginal 1–2 rows of cells occasionally have non-uniformly thickened walls), d) the ventral lobe not, or only slightly, decurrent and the lobe apex usually is broadly rounded, e) the dorsal lobe not, or only slightly, decurrent and the lobe apex usually sharply pointed (apiculate), and f) the perianth mouth smooth or with a few scattered 1–2-celled teeth.

Separation. See *S. curta* for separation from that species. See *S. mucronata* for separation from that species.

Illustrations. Damsholt 2002; Paton 1999; Schuster 1974; Smith 1990.

Habitat. On shaded soil and rocks, occasionally decaying logs. Elevation from 350 to 2000 m.

Distribution. Scapania scandica occurs in Europe, Asia, and North America. Calif. Geographic Regions: **CR**: Tehama Co. *Doyle 9413* (UC), **SN**: El Dorado Co. *Doyle 11119* (perianths) (UC).

Scapania subalpina (Nees) Dumort.

Distinctive features. These are small to large plants, 2.0–4.5 mm wide × 1–6 cm long often occurring in silt- or sand-encrusted loose tufts. The leaves usually are whitish to pale green; the stem is green to reddish-brown and blackish when mature. Look for a) dorsal and ventral leaf lobes subequal and usually distally rounded, although older leaves sometimes are more unequally bilobed than those near the shoot apex, b) margins of both lobes usually finely denticulate, occasionally smooth, c) the ventral lobe usually flat and long decurrent, d) the dorsal lobe flat to erect, nearly transversely inserted and the free margin extending across and beyond the stem, e) gemmae pale green, but pinkish to purplish-red in sun forms, and f) perianth mouth entire or finely dentate.

Separation. Small shoots of this species can resemble shoots of *S. cuspiduligera*; they can be separated by a) leaf lobe margins generally with fine marginal teeth (vs. leaf lobe margins smooth in *S. cuspiduligera*), b) larger size, shoots up to 4.5 mm wide (vs. shoots less that 2.7 mm wide), and c) keel well-developed (vs. keel not or only weakly developed). *S. subalpina* is nearly as variable in color, size and form as *S. undulata* and the two species often are difficult to separate. For separation, see discussion under *S. undulata* var. *undulata*.

Illustrations. Damsholt 2002; Evans 1923; Paton 1999; Schuster 1974; Smith 1990.

Habitat. Often near running water, but rarely permanently submerged; attached to rocks or on soil of damp ledges, banks of creeks, cascades, springs, and seepages. Elevation from 2600 to 3500 m.

Distribution. Scapania subalpina occurs in Europe, Asia, and North America. Calif. Geographic Regions: **SN**: El Dorado Co. *Doyle 11125* (UC).

Scapania umbrosa (Schrad.) Dumort.

Distinctive features. These small distinctive plants are up to 2.5 mm wide × 1.8 cm long. Shoots are whitish- or yellowish-green, or pale reddish-brown often with a purplish tinge. Growth is erect with decurved shoot tips, especially when dry. Look for a) dorsal and ventral lobes narrow, gradually tapering, and with acute apices, b) lobe margins coarsely serrate (rarely smooth), c) dorsal lobe closely lying over the ventral lobe, the lobe apex usually pointing nearly directly toward the shoot apices, transversely inserted, and not decurrent, c) ventral lobes decurrent to well below the level of insertion of the often distinctly winged keel, d) gemmae in dark- to reddish-brown clusters, and e) perianth mouth sinuate with smooth or occasionally finely dentate margins.

Separation. Scapania umbrosa is not easily confused with other species of *Scapania* (except juvenile *S. bolanderi*, which never is reddish). Distinctive are the a) erect growth, b) strongly decurved shoot apices of dry plants, c) narrow leaf lobes gradually tapering and coarsely serrate, and d) dorsal lobe tip usually pointing toward the shoot apex.

Illustrations. Damsholt 2002; Paton 1999; Schuster 1974; Smith 1990.

Habitat. Usually on damp decaying logs; also on shaded rocks and soil of paths and cliff faces; 15 to 1450 m; mostly below 600 m.

Distribution. Scapania umbrosa occurs in Europe and North America. Calif. Geographic Regions: **CC**: San Mateo Co. *Doyle 6062* (perianths) (UC), **KR**: Trinity Co. *Snodgrass 82* (DAV), **NC**: Humboldt Co. *Norris 23509* (UC), **SN**: Yuba Co. *Doyle 9588* (UC).

Scapania undulata (L.) Dumort. var. **undulata**

This species is widespread in California and remarkably variable in shape, size and coloration. Often there is little resemblance between the flaccid and undulate forms to the very rigid and non-undulate forms; yet there are intermediates between these extremes. This extreme polymorphism has led to much taxonomic confusion. Additional studies are needed to separate environmental from genetic variation.

Distinctive features. Plants are up to 5 mm wide × 20 cm long, and often form large mats or turfs. Leaves are green in shade forms, reddish-purple in the sun, and have smooth to dentate margins. Look for a) keels 0.25–0.5 of the length of the ventral lobe and without teeth, b) ventral lobes flat and long decurrent, c) dorsal lobes flat or occasionally convex, 0.35–0.65 the size of the ventral lobes, and transversely inserted or occasionally short-decurrent, d) leaf cells never with bulging trigones, and e) perianth mouth entire (usually when the leaf margins are entire) or dentate (usually when the leaf margins are dentate).

Separation. This species is most likely to be confused with *S. subalpina*. "Typical" plants of *S. undulata* can be separated from "typical" *S. subalpina* by a) unequal lobes, the dorsal lobe 0.35–0.65 the size of the ventral lobe (vs. dorsal and ventral lobes subequal, the dorsal lobe 0.75 the size of the ventral lobe in *S. subalpina*), b) dorsal lobes of well-developed leaves lying closely over the ventral lobe (vs. dorsal lobes flat to erect to squarrose), c) a shorter keel, 0.25–0.5 the length of the ventral lobe (vs. keel 0.5 the length of the ventral lobe), and d) leaves pale to dark green to reddish, to blackish (vs. leaves commonly pale to whitish-green). However, because of vegetative and perianth mouth variability, there can be times when species identification will be in doubt.

Illustrations. Damsholt 2002; Paton 1999; Schuster 1974; Smith 1990.

Habitat. Very wide range of habitats from submerged or near water-level of flowing water and cascades, to exposed summer-dry exposures; on sandy and gravelly soil, rocks, boulders, and wood. Elevation from near sea-level to 3300 m.

Distribution. Scapania undulata var. *undulata* occurs in Europe, North Africa, Asia, and North America. Calif. Geographic Regions: **CC**: San Mateo Co. *Doyle 847* (UC), **CR**: Shasta Co. *Doyle 9318* (UC), **GV**: San Joaquin Co. *MacFadden 324* (ABSH), **KR**: Siskiyou Co. *Shevock 20103* (CAS), **MP**: Modoc Co. *Doyle 9674* (UC), **NC**: Mendocino Co. *Doyle 8028* (perianths) (UC), **SC**: Riverside Co.: *Doyle 7450* (UC), **SN**: Fresno Co. *Shevock 18353* (CAS).

Scapania undulata (L.) Dumort. var. **oakesii** (Austin) H. Buch

Distinctive features. Shoots of var. *oakesii* vary from greenish, to brownish, to reddish. Shoots are 3–4 mm wide and 1.0–2.5 cm long. The presence of a conspicuous single or double row of teeth on the keel is the single most definitive feature of this variety. (**Caution:** teeth on the keel often are absent or scarce on leaves of weak stems and plants growing in wet conditions, such as during the cloudy, rainy part of the growing season. On some shoots, teeth on the keel will be present on some leaves and absent on others.) Also look for a) the dorsal lobe base often with one or more coarse teeth, b) the ventral lobe base often with teeth extending down to the decurrent strip, and c) perianth mouth denticulate.

Separation. Variety *oakesii* can be separated from var. *undulata* primarily by: a) smaller size, shoots to 4 mm wide × 2.5 cm long (vs. shoots to 5 mm wide × 20 cm long in var. *undulata*, b) keel of vegetative shoots with a conspicuous single or double row of teeth (vs. keel lacking teeth), c) dorsal lobe base often with several large teeth (vs. dorsal lobe base usually without teeth), d) teeth on the ventral lobe often extending down to the decurrent strip (vs. base of the ventral lobe usually without teeth), and e) perianth mouth denticulate (vs. perianth mouth entire or distantly toothed). Variety *oakesii* can be separated from small plants of *S. americana* by a) the presence of teeth on the keel (vs.

keel without teeth in *S. americana*), and b) a longitudinal strip of thin-walled cells in the epidermis of the ventral stem surface absent (vs. a longitudinal strip of thin-walled cells in the epidermis of the ventral stem surface present).

Illustrations. Howe 1899; Schuster 1974.

Habitat. On soil, sandstone boulders and organic matter; 30 to 2230 m.

Distribution. *Scapania undulata* var. *oakesii* occurs in North America. Calif. Geographic Regions: **CC**: San Mateo Co. *Doyle 750* (perianths) (UC), **KR**: Del Norte Co. *Frye 77* (WTU), **NC**: Mendocino Co. *Doyle 9035* (UC).

Hornworts

The hornwort gametophyte is a dorsiventral thallus lacking air-chambers and ventral scales. Diagnostic features include: a) a single large chloroplast in young cells of the apical meristem (examine the apical meristem region because some California hornworts have two or more chloroplasts in cells of older parts of the thallus), and b) a sporophyte consisting of a cylindrical capsule, a foot embedded in gametophytic tissue and a meristematic region (called an intercalary meristem) between the foot and capsule. The intercalary meristem adds new cells to the base of the capsule, resulting in a) spore mother cell differentiation occurring near the capsule base, b) meiosis and spore development occurring in the capsule middle and c) mature spore discharge occurring from the dehisced capsule apex – all occurring at the same time in a capsule.

Some California hornworts develop tubers that serve as a means to survive unfavorable conditions, such as variable rainfall and drought. Tubers are localized thickened areas containing cells filled with food-reserve. Because many tubers develop on a single thallus, tubers also are a means for population increase. The tubers can develop a) on thallus margins, b) at apices of very short to long branches, and c) on stalks on the ventral midrib region. The presence, location and size of mature tubers can aid in species identification. **Note:** tubers that develop at apices of very short branches can appear to be marginal in origin.

In California, there are 3 genera, 7 species and 1 species to be described in a subsequent publication. (The genus to which the new species to be described belongs has not yet been determined.)

Genus Key

1. Spores blackish; thallus with large mucilage- or air-filled cavities, margins often crisped; cells of antheridial walls in four tiers. . . . . **Anthoceros**
1. Spores yellow, but spores of some species turning gray-brown (fuscous) when fully mature; thallus lacking large mucilage- or air-filled cavities, margins rarely crisped; cells of antheridial wall irregularly arranged, never in four tiers. . . . . **2.**
2. Spores matured in the field mostly yellow; chloroplast with a conspicuous central pyrenoid or, if lacking conspicuous pyrenoid, with marginal tubers; antheridial chambers usually with 2 or more antheridia. . . . . **Phaeoceros**
2. Spores matured in the field gray-brown (fuscous); chloroplasts with an indistinct central pyrenoid; tubers ventral and stalked; antheridial chambers usually with 1 (seldom 2) antheridium. . . . . **Phymatoceros**

Anthoceros L. 1753
(Anthocerotaceae)

Plants of this monoicous genus usually have rather highly dissected margins with crisped margins, and the thallus dorsal surface with lamellae of variable lengths. The length of the antheridial body is important in identification of some species. Use living plants to look for antheridial chambers because they are indistinct in dry plants. The black spores usually look grayish under the compound microscope.

Three species in California.

Species Key

1. Dorsal thallus surface with numerous lamellae; distal spore face with short spines on a complex basal reticulum; proximal spore face with numerous, irregular papillae on

a simple basal reticulum, with a narrow strip devoid of papillae near the center of the triradiate ridge. . . . . **A. fusiformis**

1. Dorsal thallus surface with few to several low, short lamellae; distal spore face with short or long spines on a simple- or non-reticulate base; proximal spore face without papillae, the surface smooth with shallow to deep depressions (alveolae) that extend to the triradiate ridge. . . . . **2.**

2. Thallus dorsal surface with few or no lamellae; antheridial body (without stalk) 100–150 µm long; distal spore face with long spines, often with sharp apices. . . . . **A. punctatus**

2. Thallus dorsal surface with many low lamellae; antheridial body (without stalk) 50–90 µm long; distal spore face with low spines, often with rounded apices. . . . . **A. agrestis**

Anthoceros agrestis Paton

Distinctive features. Thalli of this monoicous species form rosettes that are less than 1.5 cm in diameter. Look for a) thalli shallowly divided into linear lobes with low lamellae on the dorsal surface usually radiating away from the rosette center, b) antheridial body 50–90 µm long, c) capsules usually to 2 (seldom to 3) cm long, d) spores 40–55 µm in diameter, e) distal spore face usually with short, unbranched spines with rounded apices, and f) proximal spore face with shallow to deep depressions (alveolae) that extend to the triradiate ridge. Mature sporophytes from April through May.

Separation. See *A. punctatus* for separation from that species.

Illustrations. Damsholt 2002; Paton 1999.

Habitat. Gravelly soil, often thin soil over granite slabs; usually shaded slow-to-dry areas in and around chaparral, coastal scrub, and margins of seepages. Elevation from 30 to 1365 m.

Distribution. Anthoceros agrestis occurs in Europe, Asia, Africa, and North America. Calif. Geographic Regions: **CC**: San Luis Obispo Co. *Doyle 5734* (UC), **SC**: San Diego Co. *Doyle 7142* (UC).

Anthoceros fusiformis Austin

Distinctive features. A. fusiformis is widespread in California and will be the hornwort species most commonly encountered. The thallus often forms a rosette of (usually) strap-shaped, overlapping branches with crisped margins. Look for a) dorsal thallus surface with numerous lamellae of variable lengths (young plants, especially, have numerous lamellae and a compact crisped appearance, and resemble gametophytes of the horsetail *Equisetum*), b) capsules with mature spores usually from 4 to over 10 cm long, c) spores mostly 42–58 (up to 62) µm in diameter, d) distal spore face with low, unbranched spines on a complex basal reticulum, and e) proximal spore face with coarse irregular papillae on a basal reticulum, the papillae do not extend to the triradiate ridge, resulting in a narrow strip on both sides of the triradiate ridge devoid of papillae and alveolae. Mature sporophytes from late March through August.

Separation. This species is separated from the other California species of *Anthoceros* by the a) large thalli with numerous dorsal lamellae, b) distal spore face with short spines on a complex reticulum and c) papillose proximal face with papillae that do not extend to the triradiate ridge.

Illustrations. Howe 1899.

Habitat. Easily disturbed summer-dry soil along trails, road banks, hillsides, landslides; exposed areas near seepages or shaded by shrubs or trees; seldom on rocks with moss. Elevation from 7 to 2340 m (the latter from Shasta Co., Doyle 9386, [UC]), but more common below 1200 m.

Distribution. Anthoceros fusiformis occurs in the Pacific Coast of Japan and North America. Calif. Geographic Regions: **CC** Santa Cruz Co. *Doyle 8155* (UC), **CR**: Shasta Co. *Doyle 9386* (UC), **GV**: Sutter Co. *Norris 103801* (UC), **KR**: Siskiyou Co. *Doyle 9217* (UC), **NC**: Lake Co. *Doyle 9078* (UC), **SC**: Riverside Co. *Doyle 7437* (UC), **SN**: Yuba Co. *Doyle 9601* (UC).

Anthoceros punctatus L.

Based on T. C. Frye collections from near Alton, Humboldt Co., Clark and Frye (1936) reported *Anthoceros punctatus* for California. WTU has two Frye collections (neither with collection number) both collected 30 July 1930 from near Alton. Examination of these collections determined that they

contained a mixture of *Anthoceros fusiformis* and *Phaeoceros carolinianus;* no thalli of *A. punctatus* were located. Although the Clark and Frye report could not be confirmed, *A. punctatus* subsequently has been confirmed for California.

Distinctive features. Living plants often are aromatic when crushed. Thalli usually form rosettes 1–3 cm in diameter. Look for a) dorsal thallus surface with few or no lamellae, b) antheridial body 100–150 μm long, c) capsules up to 10 cm long, d) spores 45–56 μm in diameter, e) a distal spore face with numerous, often sharp-pointed spines, the spines single or with 2–4 spines united at the base, and f) a proximal spore face with shallow to deep depressions (alveolae) extending to the triradiate ridge. Mature sporophytes from May through August.

Separation. Anthoceros punctatus can be separated from *A. agrestis* by a) usually forming larger rosettes, 1–3 cm in diameter (vs. thallus rosettes 0.5–1.5 cm in *A. agrestis*), b) lamellae on the dorsal thallus surface fewer and less distinct (vs. lamellae on the dorsal thallus surface many and low), c) antheridia 100–150 μm long (vs. antheridia 50–90 μm long), and d) sporophyte capsules up to 10 cm long (vs. capsules usually less than 3 cm long). Antheridial size is the surest way to separate these two species because small plants of *A. punctatus* can resemble large plants of *A. agrestis. Anthoceros punctatus* has been reported only from coastal Humboldt and Mendocino Counties; *A. agrestis* has been found in primarily coastal central and southern California. The distribution of both species needs additional field-work.

Illustrations. Paton 1999; Schofield 2002 (as *Aspiromitus punctatus*); Smith 1990.

Habitat. Damp, shaded, disturbed silty soil in garden plantings, along creek banks and shaded banks of seepages and drainages. Elevation from 8 to 75 m.

Distribution. Anthoceros punctatus occurs in Europe, Asia, North Africa, and North, Central, and South America. Calif. Geographic Regions: **NC**: Humboldt Co. *Doyle 11379* (UC) and Mendocino Co. *Doyle 10449* (UC).

Phaeoceros Prosk. 1951
(Notothyladaceae)

Thalli of this genus are light to dark green, frequently and irregularly branched, seldom with crisped margins, and without lamellae on the dorsal thallus surface. Thallus morphology is extremely variable, even in the same species when growing in different microhabitats (wet or dry, exposed or shaded, early or late in the growing season). Look for a) flat thallus branches that lack dorsal lamellae, b) antheridia 2–4 (occasionally more) per antheridial chamber, and c) spores that are yellow or brownish-yellow at maturity.

Vegetative plants of some species of this genus can be confused with vegetative plants of *Aneura, Pellia, Riccardia*, and *Blasia. Phaeoceros* can be separated a) from *Aneura, Pellia* and *Riccardia* by the presence of cyanobacteria colonies in the thallus and a single chloroplast in cells of the thallus apex (vs. absence of cyanobacteria and several chloroplasts in cells of the thallus apices of *Aneura, Pellia* and *Riccardia*), and b) from *Blasia* by unlobed thallus margins and a single chloroplast in cells of the thallus apex (vs. distinctly lobed thallus margins and several chloroplasts in cells of the thallus apex of *Blasia*).

Three species in California.

Species Key

1. Capsules short, less than 0.6 cm long; pseudoelaters mostly single cells, each cell only slightly longer than wide. . . . . **P. hallii**
1. Capsules long, up to 8 cm long; pseudoelaters often 2–4-celled, each cell usually longer than wide. . . . . **2.**
2. Chloroplasts sharply angular and with a conspicuous central pyrenoid; tubers lacking; distal spore face with numerous spines. . . . . **P. carolinianus**
2. Chloroplasts bluntly angular, or spherical, or dumbbell-shaped, or elongate, and without a conspicuous central pyrenoid; tubers common, marginal or apical; distal spore face with large crescentic to rounded warts. . . . . **P. pearsonii**

Phaeoceros carolinianus (Michx.) Prosk. ***s. l.***

Vegetative thalli and spores of *Phaeoceros carolinianus* are morphologically variable. In this publication, the species is used in a broad, inclusive sense. (See Schuster 1992b for a discussion of *P.*

carolinianus, P. mohrii, and *P oreganus*.) The vegetative thalli of California plants fall mostly within two groups: a) large thalli growing in and at the margins of permanently wet habitats, and b) smaller, more compact thalli growing in seasonally dry habitats. These differences are difficult to quantify; moreover, exceptions do occur.

Spore marking details have been used to separate populations into species. Features used include a) the number of spines across the distal spore face, b) the presence or absence of tubercles in the triangular facets between the triradiate ridge on the proximal spore face, c) tubercle distribution, clustered in the center or scattered, in the facets of the proximal spore face, d) the presence or absence of vermiculae on the distal and/or proximal spore face, and e) the width of the spore wing tissue. The details of spore markings of California populations do not fall within discrete groups. In fact, variation often occurs a) in the same population, b) in spores from the same capsule (be careful not to observe only spores that fit what you would like see), and c) spores from the same population at different times of the year. Perhaps J. Proskauer was correct: he considered the small California plants as variants belonging to the same species (personal communication). After studying this diversity and finding no clear-cut separation of variants, we are inclined to accept his judgement and refer all of these variants to *P. carolinianus*.

Distinctive features. Thalli of this strap-shaped dichotomously branched species are deep to dark green. Thallus branches and margins usually are flat, but are undulate in seepages and splash of creeks. Look for a) thalli without definite midribs, about 7–13 cells thick in the thallus mid-region, gradually thinning to 2–3 cells thick at the margins in thallus cross-section, b) tubers are not known in California plants, c) capsules up to 8 cm long, when mature splitting into two twisted valves or on one side only, d) spores yellow at maturity, 35–56 μm in diameter, e) the distal spore face with numerous short spines, and f) the proximal spore face with none, or few to many, rounded tubercles scattered or localized in the center of the facet between the triradiate ridge. Mature sporophytes from late March through October.

Separation. With its large angular chloroplast with a visible central pyrenoid, lack of tuber development, yellow spores with a spinose distal face and rounded tuberculate proximal face, this species should not be confused with other California hornworts.

Illustrations. Howe 1899 (as *Anthoceros carolinianus*); Schofield 2002 (as *Anthoceros carolinianus*).

Habitat. Shaded or open areas, permanently wet areas, such as seepages, splash of creeks, cascades and waterfalls; generally in slow to dry areas. Elevation from 6 to 1200 m.

Distribution. Phaeoceros carolinianus occurs in Europe, Asia, Africa, Australia, and North America. Calif. Geographic Regions: **CC**: Monterey Co. *Doyle 10390* (UC), **CR**: Tehama Co. *Doyle 8625* (UC), **DMoj**: Inyo Co. *Laeger 2623a* and *2594* (UC), **KR**: Del Norte Co. *Doyle 7735* (UC), **NC**: Mendocino Co. *Doyle 11376* (UC), **SC**: Riverside Co. *Doyle 7309* (UC), **SN**: Placer Co. *Doyle 11364* (UC).

Phaeoceros hallii (Austin) Prosk.

This hornwort has interesting sporophyte capsule behavior. The intercalary meristem between the foot and the capsule seems to have limited activity, resulting in a short capsule even when moisture conditions appear to be appropriate for continued cell division. The capsules often are indehiscent even when fully mature and dried naturally in the field. Field-dried capsules often are shriveled with sharp longidudinal ridges and appear immature. Dissection, however, can reveal mature spores from capsule apex to base.

Distinctive features. This is a distinctive species with thin, irregularly branched, green to light-green thalli with narrow branches mostly less that 2.5 mm wide. Look for a) a midrib region of the main branch 7–9 cells thick and a wing 1–2 cells thick in thallus cross-section, b) dry plants often with the thallus margins turned up, giving the appearance of a wide midrib, c) tubers flattened, disk-shaped, dark-green to greenish-black, usually less than 1.3 mm wide, occasionally marginal, but mostly at the apices of main or short lateral branches, d) capsules numerous, often in twos or clusters, but each with a separate involucre, e) mature capsules yellow to light-brown, less than 6 mm high, f) capsules cylindrical when fresh, but spindle-shaped and longitudinally ridged when dry, g) capsules indehiscent, or dehiscent late on one side only, h) mature spores lemon-yellow to light brown, 44–63 μm in diameter; the distal spore face with 20–35 rounded to elongate warts or low, branched ridges; the proximal spore face usually with more than 20 small, rounded papillae in the center of each facet on a matrix of interwoven fibrils between the arms of the triradiate ridge, and i) pseudoelaters mostly

unicellular, short rectangular and only slightly longer than wide. Mature sporophytes from May through August.

Separation. The gametophytes, sporophytes, and spores of this species are not easily confused with other species of the genus.

Illustrations. Frye and Clark 1947.

Habitat. Shaded soil and rocks, often with moss; slow-to-dry margins of seepages, creek banks, and humid mouse runs in tunnels under grass. Elevation from 210 to 1350 m.

Distribution. Phaeoceros hallii occurs on the Pacific Coast of North America, from Washington to California. Calif. Geographic Regions: **KR**: Trinity Co. *Doyle 8545* (UC), **MP**: Modoc Co. *Doyle 8649* (UC), **SN**: El Dorado Co. *Doyle 11363* (UC).

Phaeoceros pearsonii (M. Howe) Prosk.

Distinctive features. Plants in different microhabitats are variable in vegetative morphology and spore characteristics. In shaded, moist, slow-to-dry habitats, the thallus is green to dark green, up to 5 mm wide, and the fully mature spores usually are yellow to brownish, without secondary wall deposition, and without papillae on the proximal face. In more exposed habitats, a) the thallus is a lighter green, more highly branched and often less than 3 mm wide, and b) fully mature spores are dark brown to brownish-black (fuscous), with secondary wall deposition, and usually with few to several papillae on the proximal face.

Look for a) thalli mainly without a distinct broad central midrib region, 6–11 cells thick in the center and gradually thinning to 3–4 cells thick at the margins, in thallus cross-section , b) mature cells of the ventral thallus surface and interior tissue with angular, spherical, dumbbell-shaped, or multiple chloroplasts, c) chloroplasts without conspicuous pyrenoids, d) tubers large, flat, dark green to blackish, 2.5 mm or more wide when mature, both marginal and apical (occasionally at the apices of thin, nearly colorless branches, but never ventral in position), e) capsules up to 6 cm long, d) fully mature spores yellow, brown or brownish-black, 36–48 μm in diameter, f) the distal spore face mostly with 5–13 crescentic warts as viewed under the compound microscope or mostly round warts as viewed with the scanning electron microscope (there is a slight morphological difference between hydrated and dehydrated spores), g) the proximal spore face with interwoven fibrils and no, few or several clustered or scattered papillae, and h) pseudoelaters 1–4 cells long, and 3–8 times as long as wide. Mature sporophytes from April through June.

Separation. The combination of a) relatively large thallus, b) chloroplasts without a conspicuous central pyrenoid, c) cells of the ventral thallus surface and interior tissue with angular, spherical, dumbbell-shaped, or multiple chloroplasts, d) large marginal and apical tubers, and e) spores with 5–13 crescentic or round warts on the distal spore face separate this species from other species of the genus.

Illustrations. Howe 1899.

Habitat. Shaded soil; usually slow-to-dry summer-dry habitats; creek banks, hillsides, and road banks. Elevation from 5 to over 5000 m; mostly below 2000 m.

Distribution. Phaeoceros pearsonii occurs on the Pacific Coast of North America, from Washington to California. Calif. Geographic Regions: **CC**: San Luis Obispo Co. *Doyle 5726* (UC), **CR:** Shasta Co. *Malachowski s.n.* (CHSC 11613), **KR:** Siskiyou Co. *Doyle 5934* (UC), **NC**: Mendocino Co. *Doyle 11378* (UC), **SC**: Los Angeles Co. *Wilson 3730* (SFV), **SN**: Amador Co. *Doyle 8449* (UC).

Phymatoceros Stotler, W. T. Doyle and Crand.-Stotl. 2005
(Notothyladaceae)

Plants of this genus have a) chloroplasts that vary within thallus tissue from somewhat angular, to spindle-shaped, to somewhat rounded, to dumbbell-shaped, b) 1 (seldom 2) antheridium per antheridial chamber, and c) spores that are yellow when immature, but become fuscous when matured in the field; the darkening of the spore is correlated with the late deposition of secondary wall material on the spore surface.

P. bulbiculosus (Brot.) Stotler, W.T. Doyle and Crand.-Stotl.

Distinctive features. This species has separate female and male plants and some populations consist only of male or female plants. In the absence of sexual reproduction, the persistence of these

populations is made possible by the development of tubers. Tuber germination occurs soon after the onset of winter rains, and sex organ development begins early in young tuberlings, usually in late November to late December. Male plants are smaller than the female plants, generally less than 1 mm wide. Male plants develop a cluster of antheridia and then become vegetative and initiate development of long-stalked ventral tubers.

Female plants generally are up to 2.5 mm wide. This larger thallus, with or without sporophytes, usually is what is noticed in the field and collected. The thallus is somewhat grayish-green and often with slightly raised wing margins. The broad midrib region is 10–16 cells thick, and gradually thins to 3–5 cells thick at the wing margin, in thallus cross-section. Stalked ventral tubers develop early on female thalli without sporophytes. Plants with sporophytes develop a thickened cushion on the ventral thallus surface below the sporophyte foot; stalked ventral tubers develop later.

For *P. bulbiculosus* look for a) thalli with ventral tubers, b) erect to slightly bent capsules generally less than 2 cm tall, c) the capsule apex orange- to brownish-black, turning black as the capsules mature; the capsule usually splits on one side only, d) immature spores yellowish; mature spores brownish-black (fuscous), 47–67 µm in diameter, e) the distal spore face with a central raised elevation with thick, low circular and/or elongate ridges, and f) the proximal spore face smooth (no papillae). Fully mature sporophytes from April through June.

Separation. This is our only hornwort species that has stalked tubers on the ventral thallus surface.

Illustrations. Howe 1899 (as *Anthoceros phymatodes*); Crandall-Stotler, Doyle, and Stotler 2006.

Habitat. Shaded soil in slow to dry, summer-dry habitats. Hillsides, creek banks, road and trail banks, and margins of sloping meadows. Elevation from 15 to 650 m.

Distribution. Phymatoceros bulbiculosus occurs in Europe, and North and South America. Calif. Geographic Regions: **CC**: Santa Cruz Co. *Doyle 8384* (UC), **KR**: Shasta Co. *Doyle 9124* (UC), **NC**: Sonoma Co. *Doyle 10657* (UC), **SN**: Mariposa Co. *Doyle 8208A* (UC).

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APPENDIX I

GLOSSARY

Definition of Terms as Used in this Publication.

(See Stearn 1992, *Botanical Latin* and Magill 1990, *Glossarium Polyglottum Bryologiae* for additional definitions)

Abaxial—The surface of the leaf facing away from the axis of the stem.
Acuminate—Gradually narrowed to a slender point in leaves or leaf lobes.
Acute—Sharp pointed apex or sinus of leaves; at an angle of less than 90°.
Adaxial—The surface of the leaf facing toward the axis of the stem.
Adnate—The fusion of unlike parts to one another, such as a leaf margin to the stem.
Alveolate—With usually rounded, shallow to deep depressions.
Anterior—Toward the stem apex.
Antheridiophore—A stalk that elevates the antheridia above the thallus surface in some complex thalloid liverworts.
Antheridium (pl. **antheridia**)—Multicellular male reproductive organ in which sperm develop.
Archegoniophore—A stalk that elevates the archegonia above the thallus surface in some complex thalloid liverworts.
Archegonium (pl. **archegonia**)—Multicellular female reproductive organ, usually differentiated into a base (venter) containing an egg, and neck.
Areola (pl. **areolae**)— Angular-shaped spaces, walled by lamellae, on the surface of spores.
Auriculate—Having small ear-like lobes at the base of a leaf or underleaf.
Autoicous—Antheridia and archegonia develop on separate branches of the same gametophytic plants.

Botryoidal—Spherical clusters, like a bunch of grapes.
Bract—In leafy liverworts, a modified leaf associated with either a male or female inflorescence.
Bracteole—In leafy liverworts, a modified underleaf associated with either a male or female inflorescence.

Caducous—Detaching; in liverworts, referring to leaves and perianths that detach along pre-determined lines.
Canaliculate—Longitudinally channeled or grooved.
Capsule—The part of the sporophyte in which spores develop; the sporangium.
Carpocephalum — In complex thalloid liverworts, the female receptacle that bears sporophytes at the apex of the archegoniophore
Chlorenchyma—A tissue with chlorophyll-containing cells.
Ciliate—Having long hair-like processes.
Cismontane—The area west of the Sierra Nevada-California Cascade crest.
Columella—In hornworts, a central column of non-spore-producing tissue surrounded by spore-producing tissue.
Complicate—Leaf lobes folded face-to-face (e.g., as in *Porella* and *Scapania*).
Conic/conical—Cone-shaped, with a cylindrical base and rounded apex.
Connate—Fusion of like parts to one another, such as the tips of pseudoperianth segments in *Asterella*.
Connivent—Convergent; brought close together without fusion.
Cordate—Heart-shaped.
Cortex — In the leafy liverworts, often used for the differentiated outer layer (=epidermis): layers of stem cells that surround the non-differentiated central cells (=medulla).
Cortical—Of the cortex or outside.
Crenate—Edge scalloped with rounded teeth.
Crenulate—Slightly or minutely crenate.

Decurrent—Referring to an extension of leaf tissue down the stem below the point of insertion of the leaf on the stem.
Decurved—Broadly curved downwards or backwards towards the ventral stem surface or substrate.
Dentate—With sharp straight teeth of one or more cells in length (see serrate).
Denticulate—With minute or small teeth.
Dichotomous—Apical branching, with paired branches at least initially of equal size.
Dioicous—Antheridia and archegonia on separate gametophytes; separate male and female gametophytic plants.
Distal—In spores, the face away from the center of the tetrad of developing spores; the free outer face.
Dorsal—The morphologically upper surface of a plant; the side opposite the presence of underleaves, scales or rhizoids, or away from the substrate.
Dorsiventral—Flattened and having a distinct dorsal (top) and ventral (bottom) side.

Elaters—In sporophyte capsules, the elongate cells with helical bands of wall thickening; (see pseudoelaters).
Elliptical—Oblong with convex margins of equal length.
Emarginate—Leaf with a shallow notch at the apex; notch deeper than retuse (see retuse).
Emergent — Partly protruding, such as the extent to which the perianth protrudes beyond bracts in *Nardia.*
Epidermis — The outer cell layer of a stem or thallus (see cortex)
Explanate—Open or flattened, as in the ventral lobe of some species of *Frullania.*

Flagelliform—A branch that is either leafless or with small leaves.
Foveolate — With small pits or shallow depressions.
Fuscous—Dull- or grayish-brown.

Galeate— Term applied to specialized helmet-shaped ventral lobes in some species of *Frullania.*
Gametophyte—The haploid, gamete-producing growth phase of the bryophyte life history.
Gemma (pl. **gemmae**)—Specialized unicellular or multicellular asexual reproductive bodies.

Gemma-receptacle—Specialized structure in which gemmae develop.
Geniculate—Bent abruptly, like a knee.
Glaucous—Bluish-gray or whitish in color.
Granulate (granular, granulose)—Covered with very fine projections.
Guard cells—The pair of specialized epidermal cells that surround a pore (stoma) in the sporophyte capsule of many hornworts.

Hyaline -Translucent or nearly transparent.

Incubous—Leaf arrangement in which the front margin (toward the stem apex) of one leaf lies over the rear margin of the leaf in front of it in dorsal view (see succubous).
Incurved—A general term for curving inward or upward.
Inflexed—Abruptly bent upward.
Intercalary meristem—In hornworts, a localized region of active mitotic cell divisions located between the capsule and foot of the sporophyte.
Involucre—Strictly, a sheath of cells that grow upwards from the surface of the thallus or stem around one or more antheridia or archegonia.

Keel—A straight or curved fold or crease between the dorsal and ventral lobes of complicate-bilobed leaves; also, a ridge formed by a sharp longitudinal fold of a perianth.

Laciniate—The margin with narrow irregular lobes.
Lacunose—Having pits or depressions of variable shapes and sizes.
Lanceolate—Gradually narrowed and tapered from the base to a pointed lance-head-like apex; three or more times longer than wide.
Leaf—Lateral photosynthetic structure on stems of liverworts and mosses that is functionally analagous to the leaf of vascular plants.
Linear—Narrow with more-or-less parallel sides.
Lobule—A dimunitive lobe; often used to refer to the smaller dorsal or ventral segment of an unequally lobed leaf.
Lunate—Shaped like a crescent moon.

Marsupium—A specialized, fleshy, protective structure resulting from the downward growth of the stem apex into the substrate, carrying with it the developing sporophyte.
Medulla—The undifferentiated, central, non-cortical region of the stem in the leafy liverworts.
Meristem—Localized region of active mitotic cell division.
Midrib—The thickened, central region of thalloid liverworts, e.g., *Marchantia* and *Metzgeria*.
Monoicous—A general term to denote the development of antheridia and archegonia on the same gametophytic plant.
Monotypic—With only a single species.
Montane—Pertaining to mountains.
Mucilage hair—A short filament terminating in a cell that contains mucilage.

Nodose—With rounded, swollen knobs of cell wall thickening (as in nodose trigones of *Diplophyllum plicatum*).

Oblong—Of leaves, rectangular, with parallel sides and rounded at the apex.
Obovate—Egg-shaped in outline, with the widest part above the middle away from the stem.
Obtuse—Of leaves, blunt or rounded at the apex.
Oil-body—Translucent, opaque or colored oil-containing structure (organelle); **simple** if composed of a single unit; **compound** if composed of subunits.
Oil-cell — A cell with a single very large oil-body; common in the complex thalloid liverworts.
Orbicular—Nearly circular.
Ostiole — The opening or pore in the thallus through which sperm are released from an antheridium in some complex thalloid liverworts.
Ovate—Egg-shaped in outline (two-dimensional), with the widest part below the middle or near the base;.
Ovoid — An egg-shaped solid (three-dimensional).

Palmate—Lobes or branches radiating out as in fingers on a hand.
Papilla (pl. **papillae**)—Conical projections resembling nipples on a surface, as in papillose walls.
Parenchyma—Thin-walled tissue.
Paroicous—Male and female sex organs on the same gametophytic branch; antheridia develop immediately behind or below (away from apex) the archegonia.
Pegged rhizoids—Rhizoids with small, localized deposits of wall material (like pegs) on the inner wall surface.
Perennation—A means to persist for many years (as in tuber formation in hornworts).
Perianth—Strictly, a tubular sheath formed by the fusion of two or more modified leaves that surrounds a developing sporophyte of leafy liverworts.

Perigynium—A fleshy, tubular structure developed at the apex of a female branch after fertilization, surrounding the developing sporophyte.
Pinnate—Branches borne more-or-less regularly on either side of a stem.
Plicate—Longitudinal folds, like pleats.
Pore—An opening through the epidermis to the interior thallus tissue. 1) **compound pores:** pores surrounded by rings of superposed cells (like a barrel with open top and bottom) that project above the dorsal surface and below into the air-chamber, and 2) **simple pores:** pores surrounded by one or more concentric rings of non-superposed cells that project only above the dorsal surface.
Posterior—Away from the stem apex.
Proximal — In spores, the face toward the center of the tetrad of developing spores; the inner face.
Pseudoelater — In hornwort sporophyte capsules, multicellular or unicellular sterile cells with protoplasmic contents; false elaters (see elater).
Pseudoperianth—Strictly, a tubular sheath that develops post-fertilization from thallus tissue; each pseudoperianth surrounds a single sporophyte, e.g., *Asterella, Fossombronia*.
Punctate—With minute depressions or pits.
Pyriform—Pear-shaped.

Receptacle—Specialized sessile or stalked thallus tissue that bears sexual or asexual reproductive structures in some complex thalloid liverworts.
Recurved—Bent or curved downward in reference to the stem or thallus axis, or leaf margin.
Reflexed—Abruptly bent or curved downward or backward.
Reniform—Kidney-shaped; broadly rounded margins and a shallow sinus.
Repand—With an undulate, wavy or sinuate margin.
Reticulate—With a network-like pattern.
Retuse—A broad, shallow indentation in the otherwise truncate apex of a leaf (see emarginate).
Rhizoid—In liverworts and hornworts, a unicellular filament from the ventral surface of a stem or thallus and attaching the plant to the substrate. See also pegged rhizoids and smooth-walled rhizoids.

Secund—Leaf apices most or all turned to one side, such as the leaves of *Herbertus*.
Serrate—With teeth pointing toward the apex (see dentate).
Sexuality—See autoicous, dioicous, monoicous, paroicous.
Slime canals—Canals formed by the dissolution of end walls of files of cells that are filled with mucilage (slime).
Slime papilla—Ephemeral, thin-walled cell with swollen tip that exudes mucilage and protects the growing point.
Smooth-walled rhizoid—A rhizoid that lacks internal localized deposition (pegs) of wall material.
Spinose—Having large sharp-pointed teeth or spines.
Spinulose—Having small fine-pointed teeth or spines.
Sporangium — See capsule.
Sporophyte—The diploid, spore-producing growth phase of the bryophyte life-history.
Squarrose—Part of the leaf bent at an angle of 90 degrees or more from the rest of the leaf.
Stolon/Stoloniferous—A slender stem with or without minute leaves.
Stoma (pl. **stomata**; also called **stomate** and **stomates**)—A small pore surrounded by two guard cells leading into the photosynthetic tissue, as in the sporophyte capsule of many hornworts.
Subulate—Narrow and triangular, tapering from the base to an acute or long-acuminate apex.
Succubous—Leaf arrangement in which the rear margin of one leaf lies over the front margin of the leaf behind it in dorsal view (see incubous).
Superposed—Positioned one above the other.

Tetrad—The four haploid spores resulting from meiosis.
Thallus (pl. **thalli**)—A flattened gametophyte not differentiated into stem and leaf.
Transverse—Perpendicular to the long axis of the stem or thallus.
Trichome—A general term for an epidermal outgrowth, such as a hair or cilium.
Trigone—A cell wall thickening in the corners of cell lumens where three (or more) cells meet; of variable sizes and shapes, such as minute, large, concave, convex, bulging, and coalescent.
Triradiate ridge—Ridge on the inner face of a spore resulting from the attachment of the other three spores during spore development following meiosis.
Truncate—An apex (such as of a perianth) that ends or is folded abruptly, nearly at right angles to the main axis of the structure.
Tubercle—A small blunt (not sharp) swelling, nodule or protuberance.

Underleaf—Leaves on the morphological ventral side of the stem, as in many species of leafy liverworts.
Uniseriate—Cells in a single linear series.
Unistratose—A flat layer of cells, one cell in thickness.

Valves—Differentiated sections of the sporophyte capsule wall that separate during capsule dehiscence and spore discharge.
Ventral—The morphologically lower surface of a plant; the side bearing underleaves, scales or rhizoids, or adjacent to the substrate.

Vermiculae — Microscopic long, narrow worm-like structures.
Verrucose—Warty; with small wart-like projections.
Vinaceous—Purplish-red; wine colored.
Vitta—A row or band of longer and/or thicker-walled cells in the central part or base of a leaf and differentiated from the adjacent cells.

Wing—In vegetative plants of thalloid liverworts, the thallus tissue between the midrib region and the lateral margins. When present in spores, the area of the spore coat between the distal and proximal faces.

Appendix II

SYNONYMS

Various names historically have been applied to California liverworts and hornworts. This list of synonyms provides a crosswalk to names selected for this catalogue. The old names precede the currently accepted names.

Anthoceros carolinianus Michx. = *Phaeoceros carolinianus*
Anthoceros hallii Austin = *Phaeoceros hallii*
Anthoceros pearsoni M. Howe = *Phaeoceros pearsonii*
Anthoceros phymatodes M. Howe = *Phymatoceros bulbiculosus*
Aplozia Dumort. = *Jungermannia*
Aplozia riparia (Taylor) Dumort. = *Jungermannia atrovirens*
Aplozia sphaerocarpa (Hook.) Dumort. = *Jungermannia sphaerocarpa*
Asterella ludwigii auct. pl. = *A. gracilis*
Asterella violacea (Austin) Underw. = *A. bolanderi*
Calypogeia trichomanes auct. = *C. azurea*
Cephalozia affinis Lindb. ex Steph. = *C. lunulifolia*
Cephalozia lammersiana (Huebener) Carrington = *C. bicuspidata* subsp. *lammersiana*
Cephalozia media Lindb. = *C. lunulifolia*
Cephalozia turneri (Hook.) Lindb. = *Cephaloziella turneri*
Cephaloziella byssacea (Roth) Warnst. = *C. divaricata*
Cephaloziella byssacea var. *scabra* (M. Howe) R. M. Schust. = *C. divaricata* var. *scabra*
Cephaloziella limprichtii Warnst. = *C. stellulifera*
Cephaloziella papillosa (Douin) Schiffn. = *C. divaricata* var. *scabra*
Cephaloziella starkei (Funck ex. Nees) Schiffn. = *C. divaricata*
Cephaloziella subdentata Warnst. = *C. spinigera*
Chiloscyphus fragilis (Roth) Schiffn. = *C. pallescens* var. *fragilis*
Chiloscyphus latifolius (Nees) J. J. Engel & R. M. Schust. = *Lophocolea bidentata*
Chiloscyphus polyanthos (L.) var. *pallescens* (Ehrh. ex Hoffm.) Hartm. = *C. pallescens*
Chiloscyphus profundus (Nees) J. J. Engel & R. M. Schust. = *Lophocolea heterophylla*
Chilocsyphus rivularis (Schrad.) Loeske = *C. polyanthos* var. *rivularis*
Clevea Lindb. = *Athalamia*
Clevea hyalina (Sommerf.) Lindb. = *Athalina hyalina*
Fossombronia hispidissima Steph. = *Fossombronia longiseta*
Grimaldia Raddi = *Mannia*
Herbertus hutchinsiae auct. amer. = *Herbertus aduncus* var. *aduncus*
Jungermannia bolanderi Gottsche ex Underw. (non [Austin] Austin) = *J. confertissima*
Jungermannia danicola Gottsche ex Underw. = *J confertissima*
Jungermannia lanceolata auct. *sensu* Schrad. (non *J. lanceolata* L.) = *J. leiantha*
Jungermannia pendletonii (Pears.) A. Evans = *J. exsertifolia* subsp. *cordifolia* var. *pendletonii*
Jungermannia pumila With. var. *polaris* (Lindb.) Berggr. = *J. polaris*
Jungermannia riparia Taylor = *J. atrovirens*
Jungermannia schiffneri (Loitl.) A. Evans = *J. polaris*
Jungermannia tristis Nees = *J. atrovirens*
Kantia Lindb. = *Calypogeia*
Leiocolea alpestris (F. Weber) Isov. = *Lophozia collaris*
Leiocolea bantriensis (Hook.) Jörg. = *Lophozia bantriensis*
Leiocolea gillmanii (Austin) A. Evans = *Lophozia gillmanii*
Leiocolea heterocolpa (Thed.) H. Buch = *Lophozia heterocolpos*
Leiocolea obtusa (Lindb.) H. Buch = *Lophozia obtusa*
Leiocolea muelleri (Nees) Jörg. = *Lophozia collaris*
Lophozia alpestris auct. = *L. sudetica*
Lophozia baueriana Schiffn. = *Barbilophozia hatcheri*
Lophozia guttulata (Lindb. & Arnell) A. Evans = *L. longiflora*
Lophozia hatcheri (A. Evans) Steph. = *Barbilophozia hatcheri*
Lophozia hornschuchiana Macoun = *L. bantrienses*
Lophozia inflata (Huds.) M. Howe = *Gymnocolea inflata*

Lophozia latifolia R. M. Schust. = *L. jurensis*
Lophozia lycopodioides (Wallrich.) Cogn. = *Barbilophozia lycopodioides*
Lophozia muelleri (Nees) Dumort. = *L. collaris*
Lophozia opacifolia Culm. ex Meyl. = *L. incisa* subsp. *opacifolia*
Lophozia ovata (Dicks.) M. Howe = *Douinia ovata*
Lophozia porphyroleuca (Nees) Schiffn. = *L. longiflora*
Lunularia vulgaris Michx. = *L. cruciata*
Macrodiplophyllum plicatum (Lindb.) Perss. = *Diplophyllum plicatum*
Madotheca Dumort. = *Porella*
Madotheca cordaeana (Huebener) Dumort. = *Porella cordaeana*
Madotheca navicularis (Lehm. & Lindenb.) Dumort. = *Porella navicularis*
Madotheca roellii Steph. = *Porella roellii*
Marchantia alpestris (Nees) Burgeff = *M. polymorpha*
Marchantia aquatica (Nees) Burgeff = *M. polymorpha*
Marsupella sullivantii (De Not.) A. Evans = *M. sphacelata*
Metzgeria fruticulosa (Dicks.) A. Evans = *M. violacea*
Nardia hyalina (Lyell) Lindb. = *Jungermannia hyalina*
Nardia rubra (Gottsche) A. Evans = *Jungermannia rubra*
Neesiella Schiffn. = *Mannia*
Phaeoceros bulbiculosus (Brot.) Prosk. = *Phymatoceros bulbiculosus*
Phaeoceros laevis (L.) Prosk. subsp. *carolinianus* (Michx.) Prosk. = *P. carolinianus*
Plagiochila satoi S. Hatt. = *P. porelloides*
Plectocolea hyalina (Lyell) Mitt. = *Jungermannia hyalina*
Plectocolea rubra (Gottsche ex Underw.) H. Buch et al. = *Jungermannia rubra*
Porella rivularis (Nees) Trevis. = *P. cordaeana*
Prionolobus turneri (Hook.) Spruce = *Cephaloziella turneri*
Radula spicata Austin = *R. bolanderi*
Riccardia major Lindb. = *R. chamedryfolia*
Riccardia pinguis (L.) Gray = *Aneura pinguis*
Riccardia sinuata (Dicks.) Trevis = *R. chamedryfolia*
Riccia americana M. Howe = *R. lamellosa*
Riccia austini Steph. = *R. lamellosa*
Riccia crystallina auct. = *R. cavernosa*
Riccia lescuriana Austin = *R. beyrichiana*
Riccia minima L. = *R. sorocarpa*
Scapania bolanderi var. *americana* (Müll. Frib.) Frye & L. Clark = *Scapania americana*
Scapania granulifera A. Evans = *S. americana*
Scapania heterophylla M. Howe = *S. undulata* var. *undulata*
Scapania oakesii Austin = *S. undulata* var. *oakesii*
Scapania plicata (Lindb.) Potemkin = *Diplophyllum plicatum*
Solenostoma atrovirens (Dumort.) Müll. Frib. = *Jungermannia atrovirens*
Solenostoma cordifolium (Dumort.) Steph. = *Jungermannia exsertifolia* var. *cordifolia*
Solenostoma hyalinum (Lyell) Mitt. = *Jungermannia hyalina*
Solenostoma polaris (Lindb.) R. M. Schust. = *Jungermannia polaris*
Solenostoma pumilum (With.) Müll. Frib. = *Jungermannia pumila*
Solenostoma pumilum subsp. *polaris* (Lindb.) R. M. Schust. = *Jungermannia polaris*
Solenostoma rubrum (Gottsche ex Underw.) R. M. Schust. = *Jungermannia rubra*
Solenostoma schiffneri (Loitl.) A. Evans = *Jungermannia polaris*
Solenostoma sphaerocarpa (Hook.) Steph. = *Jungermannia sphaerocarpa*
Solenostoma triste (Nees) Müll. Frib. = *Jungermannia atrovirens*
Sphaerocarpos californica Austin = *S. texanus*

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CHARACTERIZATION OF THE ECOTONE BETWEEN JEFFREY PINE SAVANNAS AND *DARLINGTONIA* FENS IN SOUTHWESTERN OREGON

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ABSTRACT

In southwestern Oregon and northern California, Jeffrey pine (*Pinus jeffreyi*) savannas and *Darlingtonia* fens are part of a mosaic of serpentine soil-related plant communities separated by distinct ecotones. I characterized and quantified the biological and physical aspects of these transition zones. Changes in vegetation were distinguished across communities and across three sites, each a different time since fire, and water discontinuities appeared important for preserving these uniquely-adapted systems, while vegetation undergoes postfire succession from fen to shrub to savanna after approximately 100 years since fire. While many factors play a role in determining the composition and location of community boundaries, the role of water appears to be the most critical factor determining the structure and species composition of the fen and shrub communities in southwestern Oregon.

Key Words: ecotone, *Darlingtonia* fen, Jeffrey pine savanna, *Pinus jeffreyi*, transition zones.

Ecotones that separate savannas from wetland areas serve as important biogeochemical transition zones linking two distinctly different ecosystems (Johnston 1993) and promote structural and functional diversity across landscape gradients (O'Neill et al. 1986; Gosz 1993). These transition zones often reflect inherent abiotic distinctions (Johnston 1993) contributing to the development of unique plant and animal assemblages (Robertson et al. 1988; Petts 1990). Despite an increasing awareness of ecotones as functional components of landscapes (Naiman et al. 1989; Naiman and Decamps 1990; Holland et al. 1990; Gosz 1991; Hansen and di Castri 1992; Johnston 1993; Risser 1993), little is known about the mechanisms causing gradual changes in vegetation composition and structure (Kent et al. 1997) or the belowground properties responsible for discontinuous vegetation patterns across these transitional areas.

Jeffrey pine (*Pinus jeffreyi*) savannas and *Darlingtonia* (*Darlingtonia californica*) fens are part of a complex vegetation mosaic of serpentine soil-related plant communities in southwestern Oregon and northern California separated by distinct ecotones. Transition from savanna vegetation to fen vegetation reflects unique soil requirements that favor contrasting plant growth forms such as carnivorous plants (*Darlingtonia californica*), grass understory, and a pine overstory, but discourages growth of shrubs (Whittaker 1960). Although a number of species are common to both of these communities, large patches of *Darlingtonia* and sedges (e.g., *Carex mendocinensis* dominate the understory, while scattered Jeffrey pine dominate the upper canopy (Whittaker 1954; Franklin and Dyrness 1988).

The savanna-fen ecotones are distinct, both floristically and physiognomically, and can create high variability in the spatial characteristics of local plant communities. Perennial springs presumably maintain the savanna-fen ecotone in these southwestern Oregon ecosystems (Glasheen 1979; Stansell 1980), while the maintenance of similar boundaries for pine savannas in the southeastern United States is attributed to fire (Wells and Skunk 1931; Christensen 1977; Christensen 1985; Rome 1988). Although substantial changes in structure and species composition occur at the ecotone and in response to an array of environmental factors, the specific characteristics of these boundary ecotones are poorly understood.

In this paper, I characterize and quantify the physical aspects of the ecotones between Jeffrey pine savannas and *Darlingtonia* fens dominated by herbaceous species. Primarily, I test the hypothesis that a discontinuity exists between the fen and the savanna vegetation and that ecotonal vegetation structure corresponds with hydrology.

STUDY SITES

I analyzed three savanna/fen sites, each 0.5–1 ha, located within the Siskiyou National Forest in southwestern Oregon (42°07′30″N, 123°37′30″W; ≈ 700 m elevation) (Fig. 1). Within these sites both savanna and fen communities occur on lithosols with a high content of unweathered rock fragments underlain by Jurassic-aged marine sediments (White 1971; Orr et al. 1992). Surface horizons consist of weathered ultramafic rock (serpentinite and partly serpentinized peridotite) that results in a soil chemistry having: 1) high levels of exchangeable magnesium relative to other cations; 2) lower calcium levels than those found on nonserpentine soils; 3) low

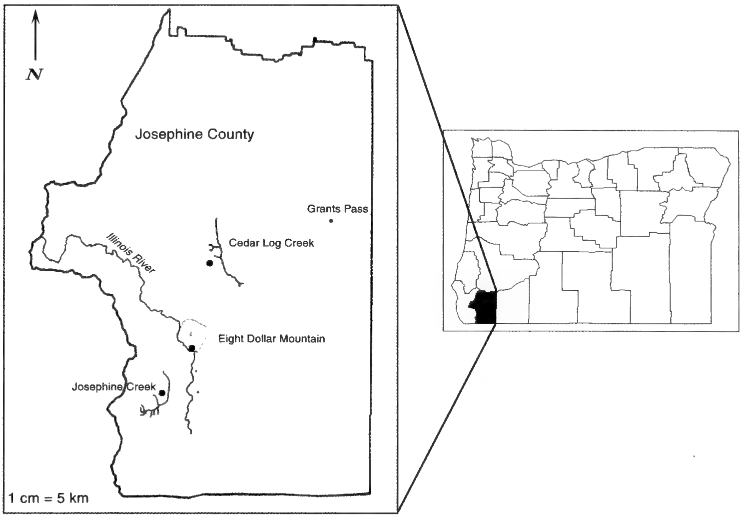

FIG. 1. Study sites, Cedar Log Creek, Josephine Creek, and Eight Dollar Mountain, located in Josephine County, Oregon.

levels of nitrogen, phosphorus, and potassium than are required for normal plant growth; and 4) high concentrations of heavy metals (chromium and nickel) with molybdenum levels insufficient for normal plant growth (Walker 1954; Kruckeberg 1984; Tolman 2004). While the savanna soils are characterized by rocky and gravelly A horizons, fen soils are considered organic belonging to a laterite clay series rich in olivine and pyroxene minerals and serpentinized to various extents giving them a dark, blue-green color (Becking 1997) with direct evidence of ground water input.

I chose my study sites for their distinct ecotones, unique vegetative requirements, and burn histories. Two of the study sites, Cedar Log Creek and Josephine Creek, included pine savanna and fen plant communities while the third site, Eight Dollar Mountain, included an intermediate shrub community between the fen and savanna. Time since last fire was: 5 years at Cedar Log Creek, 8 years at Josephine Creek, and approximately 100 years at Eight Dollar Mountain (Ulloa personal communication). Of the three sites, Eight Dollar Mountain had the longest fire-free period, a significant expanse of shrub community, and a number of endemic species. The fens ranged from 3–12 m in width and 300–600 m in length, while the savannas surrounding the fens were expansive (1–300 km^2). The sites had moderate slopes (2–10%).

The savanna vegetation is dominated by Jeffrey pine with a floristically-rich herb layer dominated by *Festuca idahoensis* (Borgias and Rudd 1999). The fens are dominated by *Darlingtonia californica* and *Carex mendocinensis* and lack trees. Typically the fens are inundated in late fall and winter, and experience drying in summer with increased evapotranspiration rates. During drought years, savanna fires burn into the fens and thus are likely to have an important role in the development of vegetative structure and composition (Agee 1991; Frost and Sweeney 2000). Fire suppression and landscape fragmentation have eliminated more extensive lightning-ignited fires in the study area (Frost and Sweeney 2000). The 1986 burn in the Josephine Creek site was a prescribed ground fire that removed all flammable herbaceous biomass and most of the accumulated litter; the fire scorched only the lower needles of pines. The 1996 burn in the Cedar Log Creek site was also a prescribed fire that burned over both communities. Both burns occurred during the late summer corresponding to the natural fire regime for the area (Borgias and Beigel 1998). All three sites were located outside the Biscuit fire of 2002.

The shrub community present at Eight Dollar Mountain is characterized by *Rhamnus californica* and *Rhododendron occidentalis* with scattered Jeffrey pine and incense-cedar (*Calocedrus decurrens*) (Whittaker 1954; Franklin and Dyrness 1988). This shrub community forms a narrow, 15 m wide band around the fen adjacent to the savanna. The area is intermediate in both hydroperiod and organic layer, slightly greater than the savanna, and slightly less than the fen, but still saturated for most of the year.

METHODS

At each of the three study sites, six transects were established perpendicular to the ecotones (Knapp 1984; Palmer and Dixon 1990) in order to locate vegetation discontinuities. Each transect contained at least nine 1 m^2 vegetation quadrats.

Transects at the Eight Dollar Mountain site extended an additional 15 m to ensure sampling of the shrub to savanna ecotone. Sample quadrat size was increased to 5 × 5 m in both the shrub and savanna communities. Sampling at the Eight Dollar Mountain site included an additional 72 sample quadrats to include the shrub community. Vegetation data were collected from a total of 227 quadrats over 18 transects. Collectively, the transects contained 2682 m^2 of sampling area.

Vegetation data were recorded throughout the growing season from June to October. Plants were identified to species where possible; nomenclature follows Hickman (1993). Some plants remained in a vegetative state throughout the season and were identified only to genus, resulting in the grouping of several species. Percent cover for each species was estimated visually using one of six cover classes (<1%, 1–4%, 5–25%, 26–50%, 51–75%, and 76–100%) (Braun-Blanquet 1965). Along each transect I recorded cover of all plant species present within each 1 m^2 quadrat and an estimated overhead foliage in both mid to upper canopies, using an imaginary 1 m^2 vertical column. I did not distinguish among all grass species, however I distinguished between grass genera.

Data Analyses

Since a primary goal of this analysis was to identify the correspondence between vegetation patterns in relation to discontinuities in gradients I used several methods to analyze vegetation gradients and discontinuities across the ecotones. An initial stratification of vegetation into two or three classes (savanna, fen, or shrub community) was made on each transect using two-way indicator species analysis (TWINSPAN) (Hill 1979). An ordination of vegetation abundance data (all transects combined) was performed using detrended correspondence analysis (DCA) (Hill and Gauch 1980) to determine compositional similarity among sites and to detect discrete clusters of quadrats. Vegetation data for the analysis were based on percent cover estimates for each quadrat along the transects.

I then used a moving split-window technique to identify vegetation discontinuities based on species composition and the principal components analysis (PCA) axis scores (Webster and Wong 1969; Ludwig and Cornelius 1987; Johnston et al. 1992). Boundary definition involves locating a discontinuity within a theoretically continuous change of vegetation. The window consisted of four sequential quadrats on a transect. Dissimilarity values between each window half (squared Euclidean distance [SED], Ludwig and Reynolds 1988) were calculated, and the window was then moved along the transect to produce a series of dissimilarity values between window halves. Dissimilarity was then plotted against quadrat position on a transect indicating abruptness in the rate of change among quadrats in species composition and PCA scores.

Additionally, I used two methods to determine and confirm the presence of hydrophytic vegetation and the boundaries of communities, both of which relied on the national list of wetland indicator plants (Reed 1988; National Resources Conservation Service 2002) (Table 1). The first method was a measure of dominance using the "50% rule" (National Research Council 1995) as the dominance ratio (Wakely and Lichvar 1997). I used a weighted average index as a second method; a modification of the prevalence index used in the 1989 federal wetland delineation manual (National Research Council 1995) based on the indicator status (OBL = 1, FACW+ = 2, FACW = 3, FACW− = 4, FAC+ = 5, FAC = 6, FAC− = 7, FACU+ = 8, FACU = 9, FAC− = 10, UP = 11) of each species in the quadrat weighted by its abundance (Wentworth and Johnson 1986; Wentworth and Johnson 1988). A priori information regarding these communities indicated threshold values to be in the range of 3–5 (Wentworth and Johnson 1986).

Physical gradients and distributions of species abundance relative to soil properties (soil texture, soil moisture, CEC, bulk density, soil nutrients NO_3 and NH_4, and organic matter, plus additional indices of water NO_3 and NH_4) were determined with canonical correspondence analysis (CCA) using CANOCO v.3.1 (ter Braak 1987) for all 227 plots. I log transformed the variables cation exchange capacity, soil pH, NO_3, NH_4, and bulk density. Soil moisture, organic matter, sand, silt, and clay and variables of vegetation abundance required square root and arcsine transformations prior to analysis to more closely approximate the assumptions of normality (Jongman et al. 1995).

Results

Environmental and Vegetation Gradients

Soil moisture and available soil nitrate and ammonium occurred as gradients across each study site. There was a notable decrease in soil moisture from fen to shrub to savanna vegetation in the Eight Dollar Mountain site with similar and significant ($P \leq 0.05$) decreases from fen to savanna communities in the other two sites (Tolman 2004). Soil moisture defined the fen in each site and dropped sharply at the ecotone preceding the savanna at each site. Soil NO_3 values were higher in the savanna, at Josephine and Cedar Log Creek, but were not significantly different from the fen levels. In contrast, soil NO_3 levels decreased from fen to savanna at Eight Dollar Mountain. The highest organic matter

TABLE 1. WETLAND INDICATOR VALUES AND SPECIES COVER DATA FOR EIGHT DOLLAR MOUNTAIN, JOSEPHINE CREEK, AND CEDAR LOG CREEK STUDY SITES (NRCS 2002). Data were recorded for quadrats along six transects at each site. Transects were between 9 and 24 m long and divided into 1 m^2 quadrats (n=227 quadrats).

Species (habitat type/ location in site)	Hydrophytic indicator	Eight Dollar Mountain range (% cover) (median)	Josephine Creek range (% cover) (median)	Cedar Log Creek range (% cover) (median)
Darlingtonia californica (perennial herb/fen)	Obligate (OBL)	2–90 (25)	8–99 (60)	1–80 (30)
Tofieldia glutinosa (perennial herb/fen)	Obligate (OBL)	0 (0)	1–10 (3)	1–40 (15)
Arctostaphylos viscida (shrub/ savanna)	Upland (UPL)	2–65 (15)	5–10 (7.5)	10–25 (15)
Agrostis spp. (graminoid/fen)	Facultative (FAC)	1–55 (5)	5–15 (5)	3–35 (10)
Carex mendocinensis (graminoid/fen)	Facultative W (FACW)	1–90 (35)	1–98 (20)	5–75 (10)
Rudbeckia californica (perennial herb/fen)	Facultative U (FACU)	7–95 (30)	1–5 (3)	2–45 (17.5)
Rhododendron occidentalis (shrub/mid-canopy)	Facultative (FAC)	1–99 (50)	0–1 (0)	2–45 (12.5)
Ceanothus pumilus (shrub/ savanna)	Upland (UPL)	1–5 (2)	5–40 (0)	1–30 (15)
Hastingsia bracteosa (perennial herb/fen)	Obligate (OBL)	3–90 (20)	1–90 (15)	10–20 (15)
Sanguisorba macrophylla (perennial herb/fen)	Facultative W (FACW)	1–45 (17.5)	1–20 (3)	2–55 (12.5)
Pinus jeffreyi (tree/savanna)	Upland (UPL)	5–199 (50)	2–50 (12.5)	2–100 (25)
Festuca idahoensis (graminoid/savanna)	Upland (UPL)	10–90 (75)	5–30 (20)	3–75 (17.5)
Calocedrus decurrens (tree/mid-canopy and savanna)	Upland (UPL)	1–60 (5)	0 (0)	5–25 (10)
Rhamnus califomica (shrub/mid-canopy)	Facultative (FAC)	1–100 (10)	0 (0)	10–65 (25)
Eriophorum crininger (perennial herb/fen)	Obligate (OBL)	0–20 (0)	0–60 (0)	0–5 (0)

values occurred in the fens at each site but were only significantly different ($P \leq 0.001$) at the Eight Dollar Mountain site. In all cases, soil NH_4 values were higher in the fen at each site but were not significantly different from the savanna values (Tolman 2004).

Distinctly separated groups of vegetation (fen and savanna) were apparent in the DCA for Eight Dollar Mountain; a strong dissimilarity gradient among quadrats occurred between the wettest and the driest sites, indicating the presence of the shrub community. Savanna and fen quadrats were clustered with little separation by either axis (Fig. 2). These sites were dominated by upland species of either *Arctostaphylos viscida, Ceanothus pumila, Festuca idahoensis* and *Agrostis* spp. for the driest sites, or by the obligate species, *Darlingtonia californica, Tofieldia glutinosa, Rudbeckia californica, Hastingsia bracteosa*, and *Carex mendocinensis* for the wettest sites. The shrub vegetation was characterized by large differences in DCA scores on both axes and was less tightly clustered than the other sites, indicating greater compositional variation among this community's quadrats. Shrub community quadrats were typically dominated by *Rhamnus californica* and *Rhododendron occidentalis,* as woody species, and *Agrostis* spp., *Rudbeckia californica*, and *Sanguisorba macrophylla* as herbaceous species.

Discontinuity in Gradients

The initial stratification of communities across the ecotones using TWINSPAN identified distinct vegetation discontinuities located between the savanna and the fen in all 18 transects at the three sites and located between the savanna and the shrub communities in the six transects at Eight Dollar Mountain (Figs. 3–6).

The CCA of species distribution indicated that vegetation was constrained by: 1) soil moisture, soil NH_4 and NO_3 (soil nutrients), organic matter, silt and CEC at Cedar Log Creek, 2) soil NH_4 and NO_3 (soil nutrients), soil moisture, sand, silt, and water NO_3 for Josephine Creek, and 3) soil moisture, soil NH_4, organic matter, and soil texture at Eight Dollar Mountain (Fig. 7). For Cedar Log Creek, CCA axis 1 depicted a soil moisture gradient, representing

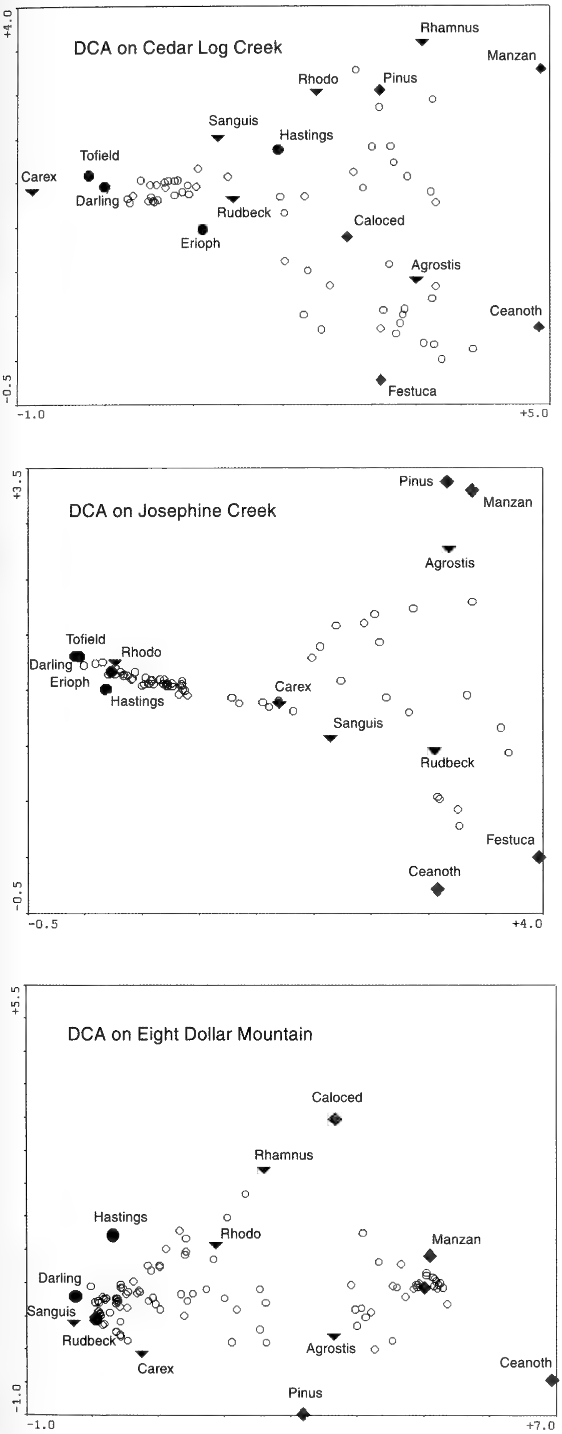

FIG. 2. Detrended correspondence of vegetation (DCA) at each site indicating community separation. Agrostis = *Agrostis* spp., Carex = *Carex mendocinensis*, Ceanoth = *Ceanothus pumila*, Darling = *Darlingtonia californica*, Festuca = *Festuca idahoensis*, Hastings = *Hastingsia bracteosa*, Manzan = *Arctostaphylos viscida*, Pinus = *Pinus jeffreyi*, Rhamnus = *Rhamnus californica*, and Rhodo = *Rhododendron occidentalis*, Rudbeck = *Rudbeckia californica*, Sanguis = *Sanguisorba macrophylla*, and Tofield = *Tofieldia glutinosa*.

54% of the variation in species distribution, whereas axis 1 for both Josephine Creek and Eight Dollar Mountain represented a nutrient gradient, explaining 46% and 73% of the variation in species distribution, respectively. Water nitrate was a more abundant nutrient than soil NH_4 at the Josephine Creek site (Tolman 2004). CCA axis 2 at Josephine Creek represented a soil textural gradient, explaining 24% of the residual variation while residual variation (19% and 23%) was explained by soil moisture and soil NH_4 gradients for Eight Dollar Mountain and Cedar Log Creek, respectively.

Environmental and vegetation discontinuities were mapped for each transect of each site (Figs. 4–6). To compare vegetation patterns in relation to discontinuities in gradients, arrows were superimposed on the x-axis to indicate results of both the 1st and 2nd CCA axes and vegetative boundary (TWINSPAN).

Peaks in the moving window analysis (squared Euclidean distance) indicated abrupt changes (high contrast values) in PCA scores (first axis). The moving window analysis of PCA scores showed sharp peaks of discontinuity within the transects at Eight Dollar Mountain more closely associated with soil qualities than with the obvious hydrology. All of the transects at Josephine Creek and Cedar Log Creek, but only two of the transects at Eight Dollar Mountain (Figs. 4–6), showed a high contrast in the center of the fen community. Broader contrast peaks along some transects (Fig. 4, transects a, c, and f, and Fig. 6, transects d and f) reflected a more gradual change and more overlap among adjacent communities.

Description of Vegetation Types

Vegetation differs distinctly between fen and savanna communities at all study sites (Fig. 8). I recorded a total of 15 species in the 6 transects at each of the three sites. Six species (40%) were perennials, two were trees, four were shrubs and two were grasses. Ten of the 15 species (66%) occurred on over half of the transects in two sites, Cedar Log Creek and Josephine Creek, and contributed to >30% of one or more community frequency values in all sites. All species were present at Eight Dollar Mountain where 27% of the species were obligate hydrophytes (OBL), 13% were facultative wetland (FACW), 20% were facultative (FAC), 7% were facultative upland (FACU), and 40% were upland (UP). Vegetation was significantly hydrophytic in all three fens (57% OBL) while the savannas were comprised of upland dominants (70% UP).

I used a threshold value of 4 for the prevalence index to indicate the presence of hydrophytic vegetation; values above 4 were considered either shrub or savanna vegetation types. This boundary criterion was consistent with contrast values

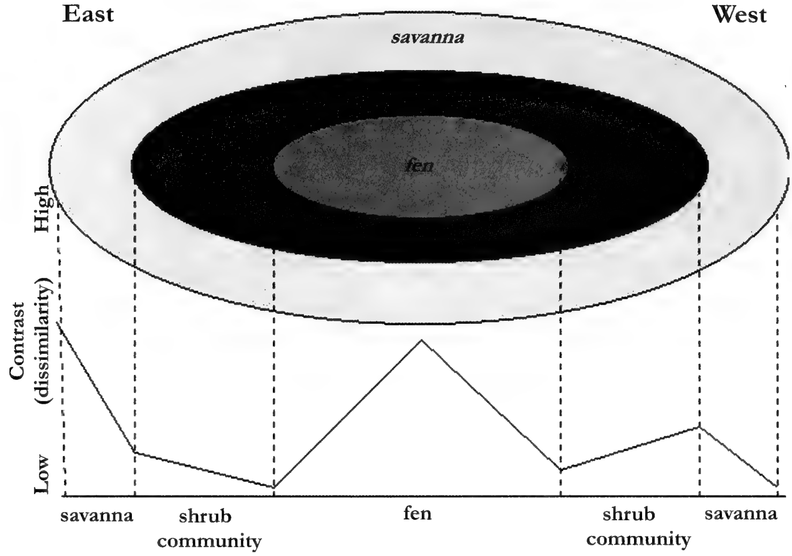

FIG. 3. Generalized plan view of the Eight Dollar Mountain site illustrating quadrat location along a transect through the site. The moving window results illustrate the hypothesized location of high contrast values.

of soil texture, nutrients, and hydrologic conditions for hydrophytic vegetation in the Josephine and Cedar Log Creek sites. However, at the Eight Dollar Mountain site, this criterion was only consistent with soil moisture boundaries. I found the 50% rule method for determining the presence of hydrophytic vegetation inconsistent in determinations of discontinuities between the shrub community and the fen but consistent in determining the discontinuity between the shrub community and the savanna. Discontinuities indicated by this method often matched the prevalence index boundaries, except where transects contained a shrub community. Hydrophytic vegetation boundaries determined by the prevalence index were not closely associated with vegetation compositional discontinuities identified with TWINSPAN (Figs. 4–6).

Differences in median percent cover were greatest between communities at each site, with fens having a greater percent cover than the savannas. *Darlingtonia californica, Rudbeckia californica,* and *Sanguisorba macrophylla* were the most common fen species. *Darlingtonia, Hastingsia bracteosa, Rudbeckia californica*, and *Carex mendocinensis* represented one half of the total plant cover, while *Festuca idahoensis, Pinus jeffreyi*, and *Arctostaphylos viscida* dominated the savanna at the Eight Dollar Mountain site. The dominant shrub species at the Eight Dollar Mountain site were *Rhamnus californica* and *Rhododendron occidentalis. Sanguisorba macrophylla*, *Rudbeckia californica*, and particularly *Carex mendocinensis* were common in the adjacent communities at all three sites.

Carex mendocinensis was an important and spatially variable component of ground cover species at the three sites. At Cedar Log Creek and Eight Dollar Mountain, *Carex mendocinensis* decreased toward the savanna end of the moisture gradient along the transects. However, at the Josephine Creek site, the persistence of *Carex mendocinensis* obscured differences between savanna and fen communities in 30% of the quadrats (Fig. 8).

Both the dominance ratio for hydrophytic vegetation and the species prevalence index values (based on weighted averages) were consistent for savanna and fen communities at all three sites. Non-parametric median comparisons (Kruskal-Wallis H-test) showed that fens differed significantly ($P \leq 0.001$) from savannas for all three sites. Differences between the dominance ratio and the prevalence index identified the shrub community quadrats at Eight Dollar Mountain (National Research Council 1995; Wakely and Lichvar 1997) indicating that the indices reliably separated hydrophytic from non-hydrophytic plant communities. Floristic similarity in each community, based on 15 indicator species, changed significantly ($P \leq 0.001$) from fen to savanna communities in the Cedar Log Creek and Josephine Creek sites while at Eight Dollar Mountain the significant change ($P \leq 0.001$) was from savanna to shrub community. Variations in slope had no impact along transects at the sites.

In summary, the analyses TWINSPAN and moving windows, indicated that hydrophytic vegetation does not determine vegetation type discontinuities with the exception of fen vegetation at the Eight Dollar Mountain site (100 years since the last burn). While the prevalence index and the DCA consistently separated all vegeta-

tion types for each site, TWINSPAN and moving windows indicated that the fen and the shrub communities could not be separated. The 50% rule was the only analysis that consistently failed to separate vegetation types at a site.

Discussion

To the casual visual observer, composition and structure of the ecotone boundaries at Cedar Log Creek and Josephine Creek appear sharp and distinct between the fen and savanna vegetation types. Eight Dollar Mountain contains equally distinct ecotones with its inclusion of a third distinct shrub vegetation type. Statistical examination, however, reveals high species turnover rates (gradient lengths of 3.9 to 4.3) between communities insufficiently different to be considered abrupt boundaries (van der Maarel 1976; Hobbs 1986). Recent interpretations of community dynamics suggest that the environmental discontinuities underlying these systems may characterize them as communities in transition (Hobbs 1986).

Traditionally, narrow ecotones have been identified by two key characteristics: 1) large differences in DCA scores between two communities (a separation of clusters) and 2) a high species turnover rate (between 10 and 25.5 Half Changes (HC)/100 m) (Hobbs 1986) or a change in species composition between communities within a short distance. Among my sites, DCA scores for Eight Dollar Mountain depicted tightly clustered and separated fen and savanna vegetation while the shrub community contained plants common to both extremes. TWINSPAN recognized only shrub vegetation and savanna; and did not recognize the fen as a separate and distinct vegetation type. Although gradient lengths are sufficiently high to be considered unimodal (Tolman 2004), HC values, used to calculate beta diversity (Gauch and Whittaker 1972), are less than the 10 to 25 HC/100 m needed to distinguish the shrub community as a separate community (Hobbs 1986). Species turnover rates are low, thus the shrub-dominated area at this site meets Hobbs' (1986) criterion for a *discontinuous transition* or van der Maarel's (1976, 1990) criterion for a "*limes divergens*". In a "*limes divergens*" case, the boundaries are vague since a gradual change in environmental conditions results in populations that gradually merge into one another.

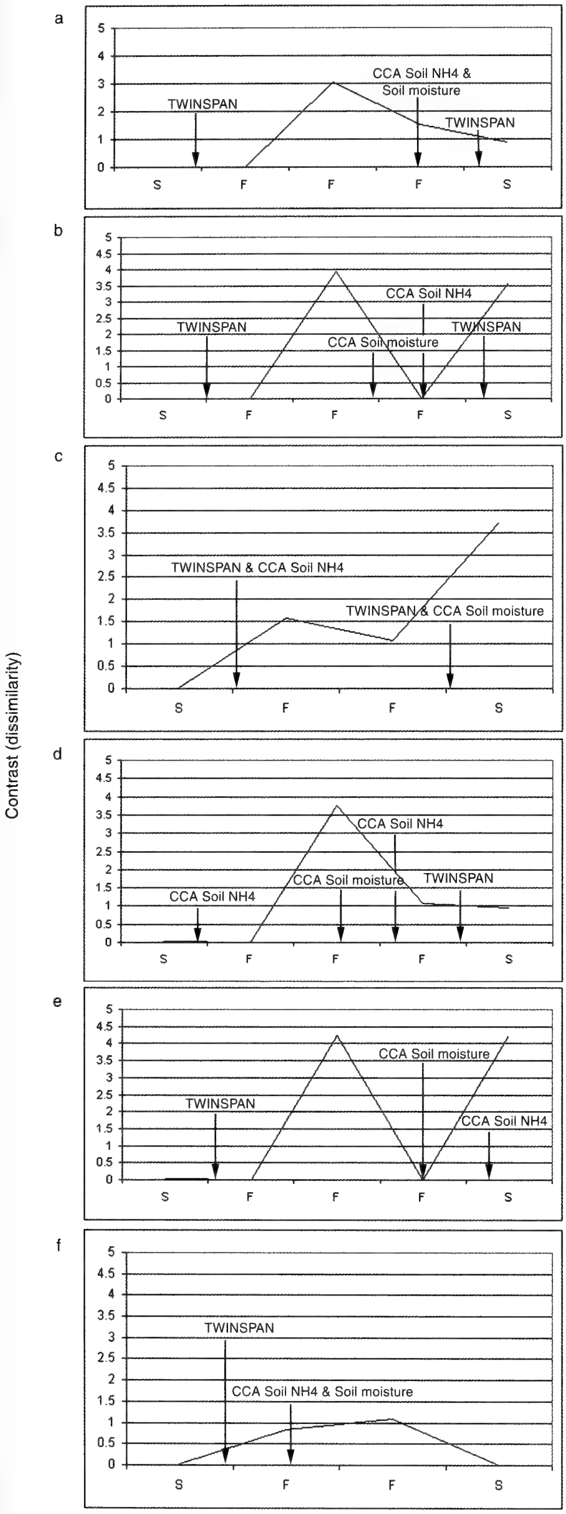

FIG. 4. Each transect (a–f) of the Cedar Log Creek site illustrating high contrast values of the moving window analysis along the transect. Arrows on the x-axis indicate hydrology (1st CCA axis) and soil ← nutrients (2nd CCA axis), and the vegetative discontinuity (TWINSPAN). Peaks in the moving window analysis (squared Euclidean distance) indicate abrupt changes (high contrast values) in PCA scores. S = savanna, F = fen.

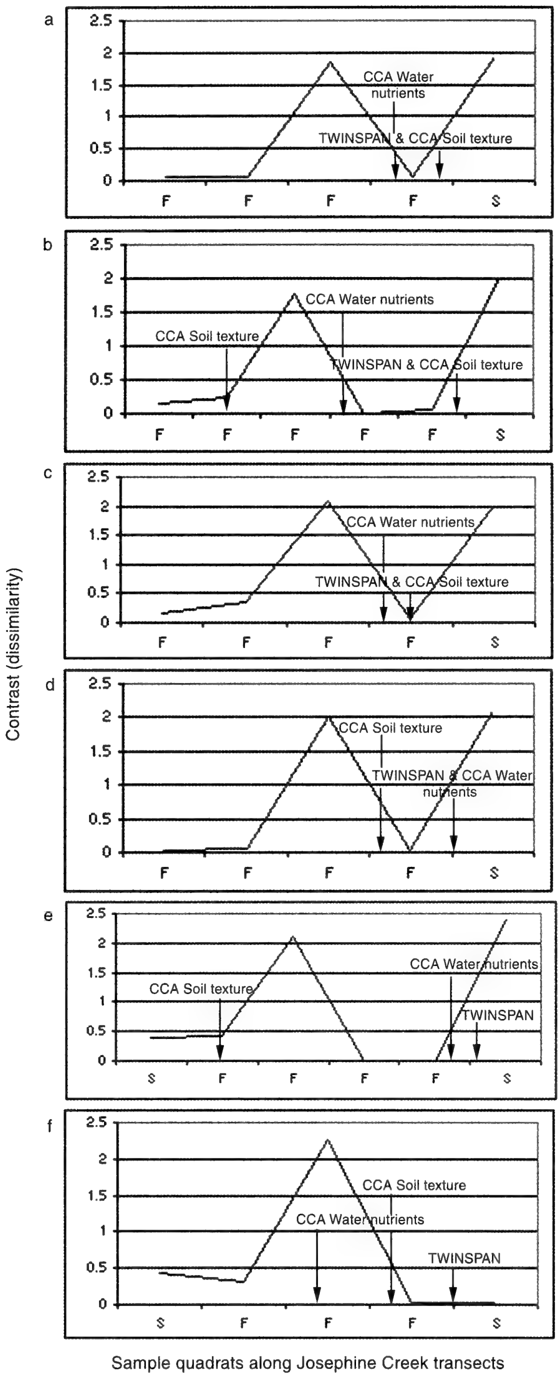

FIG. 5. Each transect (a–f) of the Josephine Creek site illustrating high contrast values of the moving window analysis along the transect. Arrows on the x-axis indicate water NO_3 (1st CCA axis) and soil texture (2nd CCA axis) and the vegetative discontinuity (TWINSPAN). Peaks in the moving window analysis (squared Euclidean distance) indicate abrupt changes (high contrast values) in PCA scores. S = savanna, F = fen.

DCA scores for both Josephine and Cedar Log Creek depicted only the fen as tightly clustered and distinctly separated; savanna vegetation exhibited a strong gradient of increasing dissimilarity among its quadrats. These results contrast with those of the prevalence index and 50% dominance rule, which along with the TWINSPAN analysis separates fens from the savanna. However, low species turnover rates, along environmental gradients at all three sites supports an ecotone interpretation similar to those of Hobbs' (1986) and van der Maarel (1976) as previously observed for the site at Eight Dollar Mountain.

One half the transects at the Eight Dollar Mountain and the Cedar Log Creek sites were related to soil moisture and soil nutrients, with the exception of five transects (Fig. 4, transects a, c, and f, and Fig. 6, transects d and f). At the Josephine site, vegetation boundaries and water nutrients were more closely aligned. Together, these results are insufficient to fully interpret the processes responsible for changes that may be occurring at the boundary but support van der Maarel's (1976) theory that water, as a disturbance factor, creates a zone of fluctuating environmental conditions. Water availability, within this context, could result in specific chemical and/or physical attributes that may influence interactions between adjacent vegetation types at the ecotones. Thus, the general distinction of these ecotones would lie in their location relative to the reduced kinetic energy of the stream adjacent to the fen (Wiens et al. 1985; Forman and Godron 1986; Holland 1988; Naiman et al. 1989). Theoretically, water influences the boundary by deflecting sediment and organic matter to the edges, causing changes in the physical and edaphic gradients all along the edge of the fens (Forman and Godron 1981) or "permeability" of the membrane as identified by Wiens et al. (1985).

Hypothetically, significant amounts of organic matter could accumulate at the boundaries between the fen and the savanna community at each site with water flow altering soil characteristics at the fen boundary by slowing and dispersing any sediment to the community edge. Research with boundaries and beaver impoundments show this process facilitates the development of community structure at pond edges (Johnston and Naiman 1987). The work of Cadenasso et al. (1997) in upland forests with edges and gradients shows a similar effect related to sidewall vegetation that alters abiotic factors more dramatically than expected. Van der Maarel's (1976) ecotone research would suggest that Cedar Log Creek and Eight Dollar Mountain exemplify communities with sites that may converge floristically, given enough time. My results appear to support van Leeuwen's (1966) prediction that species such as those found in the shrub community may reside in transitional zones

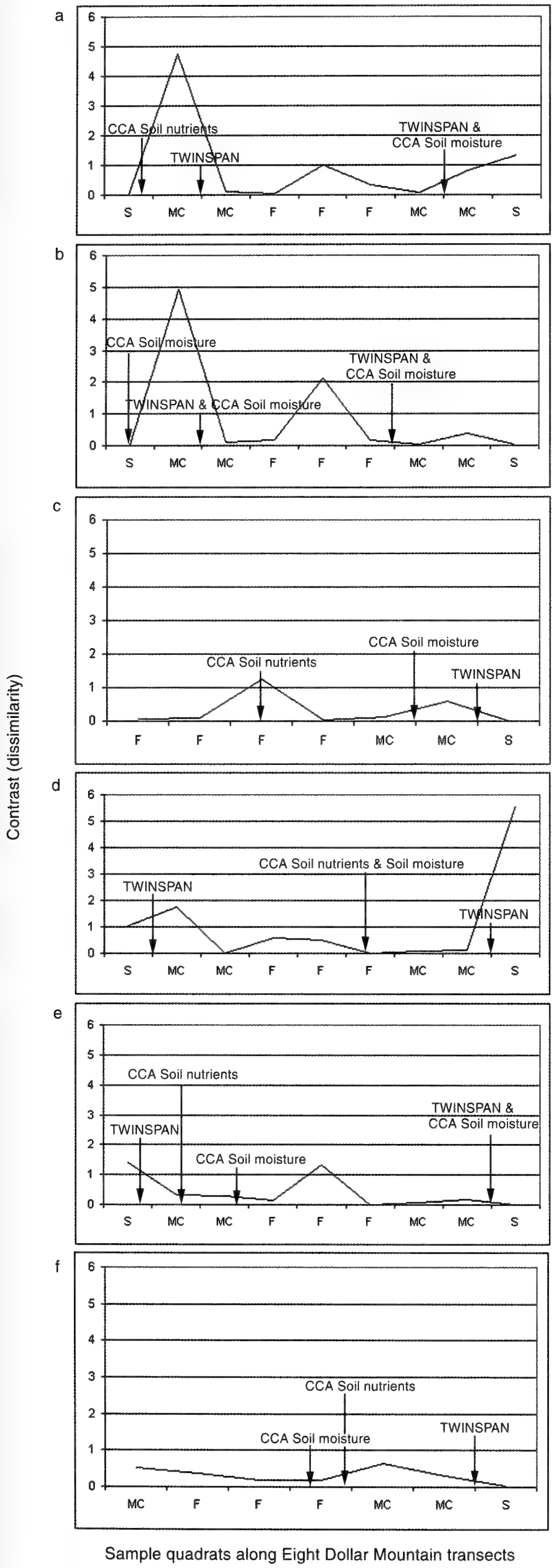

FIG. 6. Each transect (a–f) of the Eight Dollar Mountain site illustrating high contrast values of the ← moving window analysis along the transect. Arrows on the x-axis indicate soil nutrients (1st CCA axis) and hydrology (2nd CCA axis) and the vegetative discontinuity (TWINSPAN). Peaks in the moving window analysis (squared Euclidean distance) indicate abrupt changes (high contrast values) in PCA scores. S = savanna, F = fen, MC = shrub community.

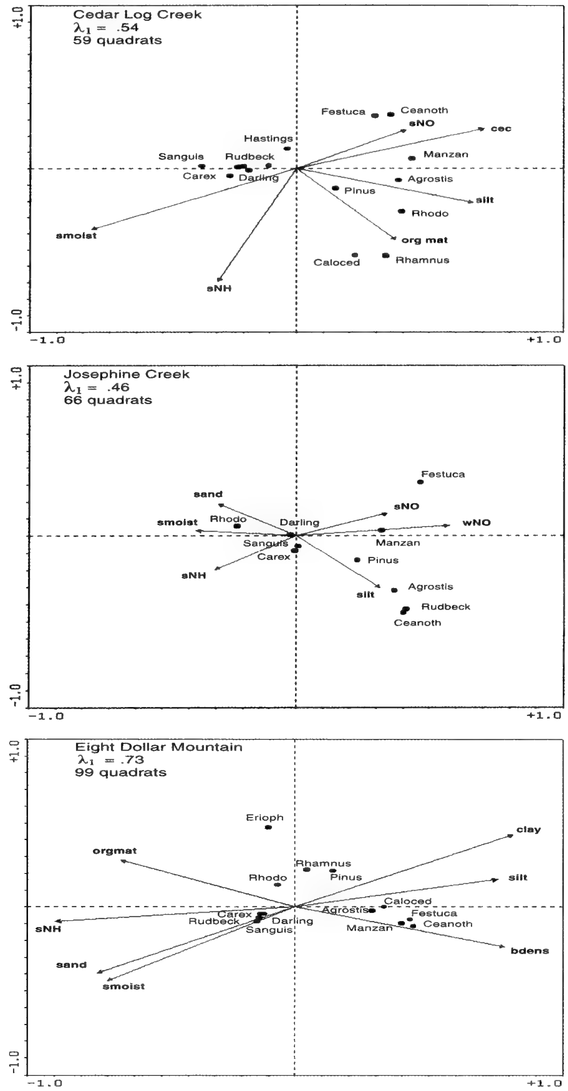

FIG. 7. Canonical correspondence analysis results of transect quadrats by site. Smoist = gravimetric soil moisture, orgmat = organic matter, bdens = bulk density, sNH = soil NH_4, sNO = soil NO_3, and wNO = water NO_3.

associated with unstable environments. This may be especially true of Josephine Creek where sediment may not be sufficient enough to alter the soil characteristics at the edge.

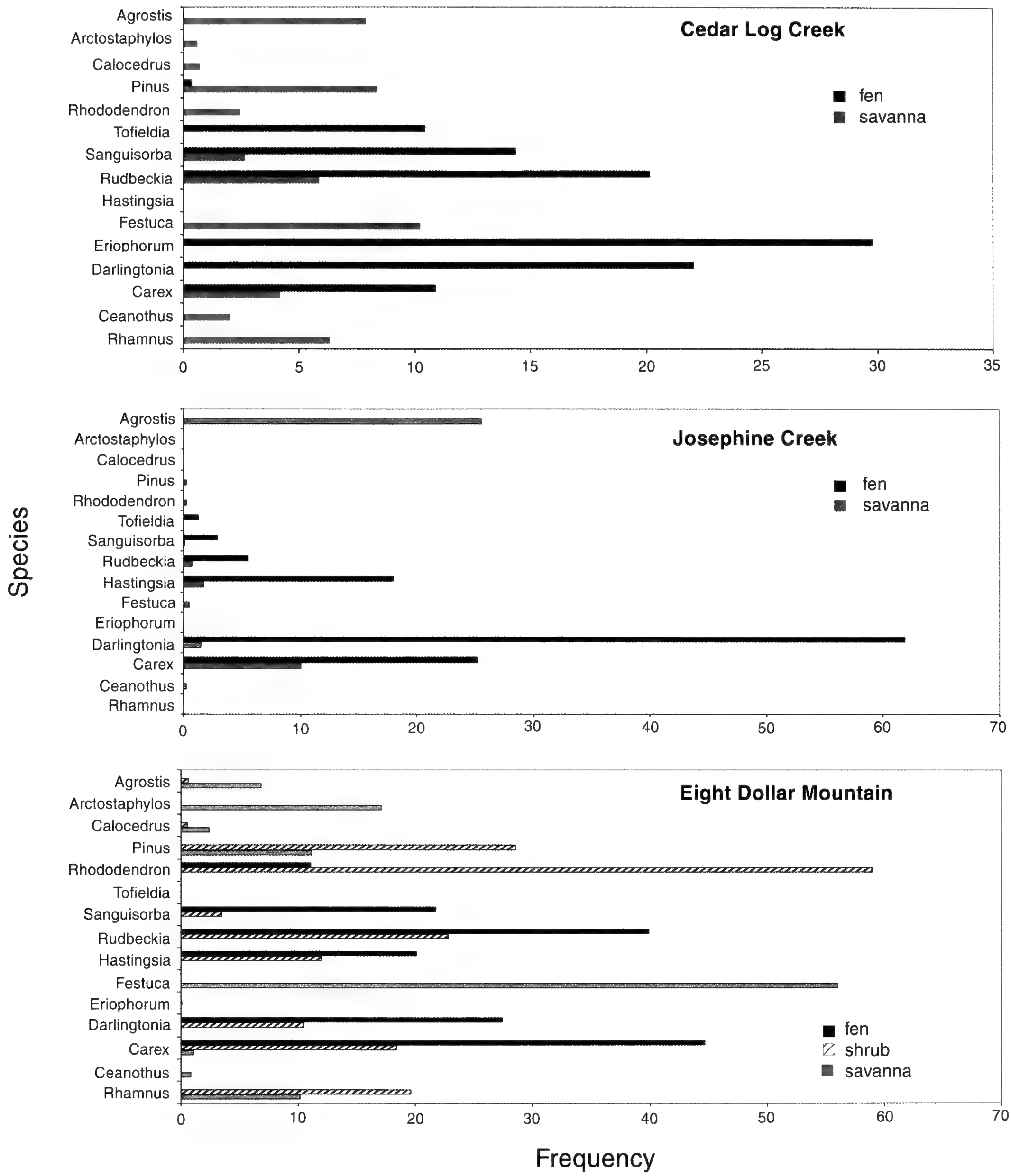

FIG. 8. Species composition across the savanna, shrub, and fen communities at Cedar Log Creek, Josephine Creek, and Eight Dollar Mountain study sites.

CONCLUSION

Where many factors play a role in determining the composition and location of community boundaries, the role of water appears to be the most critical factor determining the fate of the fen and shrub communities in southwestern Oregon. Differences in soil structure and chemistry from the fens to the savannas at all three sites may well be the result of processes that can influence decomposition and nutrient cycling characteristics at the ecotone level (Gosz 1981; Berg and McClaugherty 1987). As succession proceeds, fluctuating water tables lead to two possible outcomes: 1) either an increase in soil moisture levels, or 2) a decrease in soil moisture levels that enables adjacent species to occupy the boundary zone and alter the microhabitat. If sidewall vegetation should establish and further ameliorate the ecotone, this would explain the lack of differentiation between the fen and shrub community at Eight Dollar Mountain and the high contrast in the stream center at Josephine and Cedar Log Creek. These processes may well play

a role in determining the rate of *Carex mendocinensis* invasion in these sites and the rate of community differentiation. Although studies at broader scales average the local (fine-scale) heterogeneity and are more predictable (O'Neill et al. 1986), small-scale disturbance events such as sediment movement play key roles in releasing local nutrients, promoting patch scale recruitment of seedlings and ameliorating the soil at the ecotones. These small-scale processes have been known to turn subtle changes in the environment into measurable ecosystem responses (Gosz and Sharpe 1989).

ACKNOWLEDGMENTS

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VASCULAR FLORA OF THE TENDERFOOT CREEK EXPERIMENTAL FOREST, LITTLE BELT MOUNTAINS, MONTANA

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ABSTRACT

Tenderfoot Creek Experimental Forest (TCEF) is situated in the Little Belt Mountains of Montana, 120 km east of the Continental Divide. TCEF is composed of 3693 ha at elevations between 1840 and 2420 m and is dominated by lodgepole pine forest, which covers about 3366 ha, with interspersed floristically rich meadows. Our floristic inventory is based on collections and field observations made by Scott Mincemoyer during 1996–1999 and collections by Jennifer Birdsall during 2003–2005. We also include collections made by Earle Layser in 1992 and Jessica Fultz in 2002–2003. The vascular flora of TCEF consists of 312 species, representing 162 genera and 44 families. Twenty-seven exotic species occur in TCEF including *Centaurea maculosa, Chrysanthemum leucanthemum, Cirsium arvense*, and *Tanacetum vulgare* which are listed as noxious weeds in Montana. *Phlox kelseyi* var. *missoulensis* is found in the experimental forest and is listed as sensitive by the USDA Forest Service Northern Region.

Key Words: Tenderfoot Creek, Little Belt Mountains, Montana, plant inventory, vascular flora.

Tenderfoot Creek Experimental Forest (TCEF) was established in 1961 on the Lewis and Clark National Forest for the purpose of watershed research. TCEF is situated 40 km due north of the town of White Sulfur Springs in Meagher County, Montana in the Little Belt Mountains which are 120 km east of the Continental Divide. TCEF is located at approximately 46°55′N latitude and 110°52′W longitude and includes portions of T13–14N, R6–7E. TCEF encompasses the headwaters of Tenderfoot Creek, a west flowing tributary of the Smith River, and consists of 3693 ha at elevations between 1840 and 2420 m (Schmidt and Friede 1996). The watershed comprises seven subdrainages running north-south in a dendritic pattern (Barrett 1993). Included within TCEF is the Onion Park Research Natural Area (RNA) which was established in 1991. Onion Park RNA comprises 474 ha dominated by a floristically rich wet meadow complex in the upper portion of the watershed (Layser 1992). The RNA also includes surrounding forests and a majority of Quartzite Ridge (Fig. 1). Schmidt and Friede (1996) details the climate, geology, and soils of TCEF.

Climate

According to Schmidt and Friede (1996), TCEF is dominated by a continental climate influenced by the mountainous topography. Rainfall averages 880 mm with a range of 594 to 1050 mm from the lowest to the highest elevations. Precipitation usually peaks during the winter months at 100 to 125 mm per month and averages 50 to 60 mm per month during July through October. Temperatures can go below freezing every month of the year, thus the average growing season is fairly short. The season averages a low of 30 to 45 days on the higher ridges and 45 to 75 days at lower elevations (Schmidt and Friede 1996).

Geology and Soils

Schmidt and Friede (1996) describe TCEF as characterized by igneous intrusive sills of quartz porphyry, Wolsey shales, Flathead quartzite, and granite gneiss. The northern part of TCEF occupies the highest elevations and steepest upland topography and is underlain by igneous intrusive granitic rocks. The arched bedrock in the area was formed from metasediments of Cambrian Age consisting mainly of argillites and quartzites. Glaciation has influenced the landform, producing broad basins in which the streams are beginning to regain a water-carved dendritic pattern. Tenderfoot Creek has carved the deepest pattern and is entrenched in a steep canyon with prominent bedrock cliffs. The most

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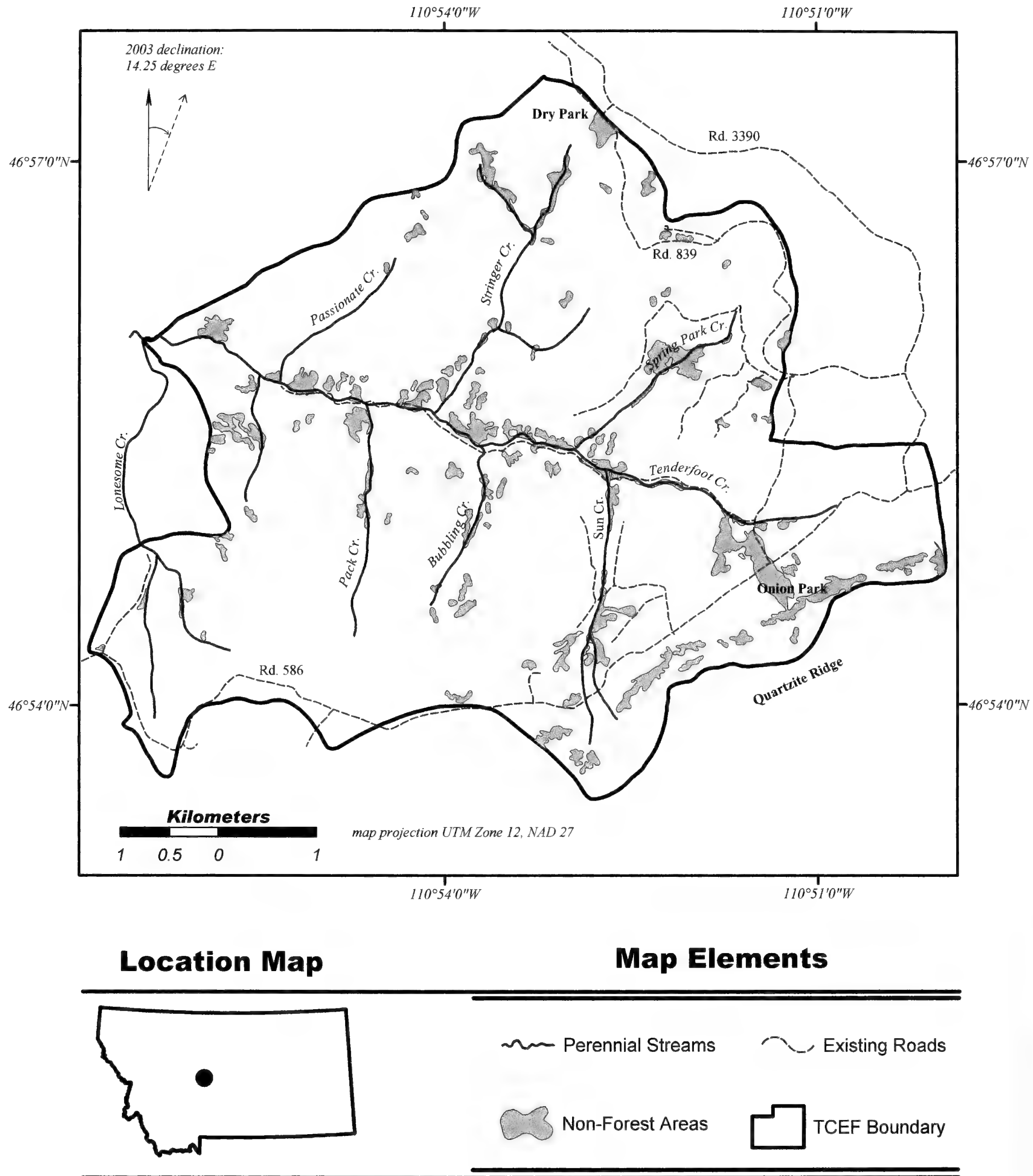

FIG. 1. Location and map of Tenderfoot Creek Experimental Forest, Meagher County, Montana. (Prepared by Rob Ahl, formerly of the USFS, Rocky Mountain Research Station, Missoula, MT 59807 and now at the University of Montana, College of Forestry and Conservation, Missoula, MT 59812).

extensive soil groups are the loamy skeletal, mixed Typic Cryochrepts and clayey, mixed Aquic Cryoboralfs. Rock talus slopes are prominent on the perimeter, but rock outcrops are confined chiefly to areas adjacent to main stream channels. Grassland parks are prominent at the heads of the drainages. Soils in the parks range from well to poorly drained. Seeps and springs are common.

Plant Communities

The study area falls within the subalpine or Hudsonian life zone of Merriam and is dominated by lodgepole pine, which covers about 3366 ha. Other habitats of considerable size include 125 ha of floristically-rich wet meadows and 54 ha of open, grassy or rocky slopes (Schmidt and Friede 1996). Forested communities are domi-

nated by even-age lodgepole pine stands with low species diversity. Late seral or more mesic stands may have a significant component of subalpine fir and/or Engelmann spruce in the understory or overtopping the lodgepole pine.

Five forested habitats described by Pfister et at. (1977) account for the majority of the area in TCEF. These five types in order of abundance are:

1. *Abies lasiocarpa*/*Vaccinium scoparium* habitat type—occurs on most well-drained, mid to upper slopes.
2. *Abies lasiocarpa*/*Vaccinium globulare* habitat type—occurs on slopes at low to mid elevations.
3. *Abies lasiocarpa*/*Calamagrostis canadensis* habitat type—occurs on moist swales, slopes and draws.
4. *Abies lasiocarpa*—*Pinus albicaulis*/*Vaccinium scoparium* habitat type—limited mainly to the ridge on the northeast border above 2380 m.
5. Forested Scree—occurs mainly along Quartzite Ridge and on other slopes scattered throughout the drainage. This may better be described as *Abies lasiocarpa*/scree habitat type in most of the study area.

In addition to the five types mentioned, twelve grassland or riparian types have been mapped by Layser (1992) in Onion Park RNA. Most, if not all, of the non-forested sites in TCEF would fall into these vegetation types. However, the nomenclature of a few of the species that define the types mapped by Layser is now considered out of date. *Agropyron caninum* is called *Elymus trachycaulis* in most newer floras, including Dorn (1984), and *Carex utriculata* is the updated name for the taxa previously referred to as *Carex rostrata* throughout much of the west. The true *Carex rostrata* is a boreal species and is rare in Montana (Reznicek 1997). Types with either of these names could be relabeled with their currently accepted names, though we have retained the original nomenclature herein. The non-forested types mapped by Layser are:

1. *Deschampsia cespitosa*/*Carex spp.* habitat type—most common seasonal wetland type. Described by Meuggler & Stewart (1980).
2. *Festuca idahoensis*/*Deschampsia cespitosa* habitat type—common in drier areas than *Deschampsia cespitosa*/*Carex spp.* ht. Described by Meuggler & Stewart (1980).
3. *Festuca idahoensis*/*Agropyron caninum* habitat type, *Geranium viscosissimum* phase—more mesic than the typic phase, probably limited in distribution to Onion Park and Dry Park. Described by Meuggler & Stewart (1980).
4. *Eriophorum chamissonis*/*Carex spp.* community type—occurs in very wet sites, limited to Onion Park and Sun Creek areas. Previously undescribed type in Montana (Layser 1992).
5. *Alopecurus alpinus*/*Carex spp.* community type—probably limited to Onion Park. Previously undescribed type in Montana (Layser 1992).
6. *Deschampsia cespitosa*/*Carex spp.* habitat type wet phase—more mesic phase of habitat type. Undescribed phase of *Deschampsia cespitosa*/*Carex spp.* habitat type.
7. *Mertensia ciliata*/*Senecio triangularis* community type—minor type next to springs, seeps and rivulets. Would now key to *Senecio triangularis* community type in Hansen et al. (1995).
8. *Festuca idahoensis*/*Agropyron caninum*/*Melica spectabilis* habitat type—minor type in Onion Park and probably elsewhere in TCEF. Previously undescribed type, but would key to *Festuca idahoensis*/*Agropyron caninum* habitat type in Meuggler & Stewart (1980).
9. *Carex rostrata*/*Deschampsia cespitosa* habitat type—occurs in wet areas adjacent to streams or springs on in seeps. Described by Hansen et al. (1995).
10. *Salix geyeri*/*Carex rostrata* habitat type—occurs adjacent to streams, springs, seeps and rivulets. Would now key to *Salix drummondiana*/*Carex rostrata* habitat type in Hansen et al. (1995)
11. *Salix geyeri*/*Calamagrostis canadensis* habitat type—occurs adjacent to streams, springs, seeps and rivulets. Would now key to *Salix drummondiana*/*Calamagrostis canadensis* habitat type in Hansen et al. (1995).
12. *Picea engelmannii*/*Salix spp.*/*Carex spp.* community type—occurs adjacent to streams, springs, seeps and boggy areas. Would now key to *Picea spp.*/*Calamagrostis canadensis* community type in Hansen et al. (1995).

Development of Flora

The flora is mainly based on collections and field observations made in 1996–1999 by Scott A. Mincemoyer and 2003–2005 by Jennifer L. Birdsall. Collection dates in 1996 included time spans throughout the field season. 1997 collecting was limited to June 23–26 and August 13–15. 1998 was limited to June 27–28 and August 8–9. 1999 was limited to July 13–15. 2003 was limited to July 28–30. 2004 was limited to August 17–19. 2005 was limited to August 23–25. Collections by Earle F. Layser in August, 1992 in Onion Park RNA are included in the flora as are collections made by Jessica E. Fultz during the summers of 2002 and 2003. A search of the MRC herbarium

(Rocky Mountain Research Station, Forestry Sciences Laboratory, Missoula, MT) for additional specimens resulted in three vouchers collected by Frank A. Clark in 1914 and 1915 in Onion Park. Taxa previously reported for TCEF or Onion Park RNA by others are not included in the main body of the flora since no voucher specimens were collected and some reported taxa are believed to be outside of the boundary of the experimental forest. However, these taxa are listed separately and their presence in TCEF should be sought and documented if possible.

Floristic Summary

The vascular flora of TCEF consists of 312 species, representing 162 genera and 44 families (Tables 1–3). Twenty-seven exotic species occur on the experimental forest. These are: *Arabis glabra, Artemisia absinthium, Bromus inermus, Carduus nutans, Centaurea maculosa, Chrysanthemum leucanthemum, Cirsium arvense, Cirsium vulgare, Dactylis glomerata, Filago arvensis, Lactuca serriola, Medicago lupulina, Melilotus officinalis, Phleum pratense, Poa pratensis, Polygonum convolvulus, Rumex acetosella, Sonchus arvensis, Spergularia rubra, Tanacetum vulgare, Taraxicum laevigatum, Taraxicum officinale, Thlaspi arvense, Tragopogon dubius, Trifolium hybridum, Trifolium pratense*, and *Trifolium repens*. The nativity of two species, *Festuca rubra* and *Poa palustris*, is uncertain. *Centaurea maculosa, Chrysanthemum leucanthemum, Cirsium arvense*, and *Tanacetum vulgare* are listed as noxious weeds by the Montana Department of Agriculture. Their distributions in TCEF are limited to a few scattered individuals or small clumps mainly along roads and in meadows adjacent to roads. *Phlox kelseyi* var. *missoulensis* is the only documented rare species in TCEF and is listed by the USDA Forest Service Northern Region as a sensitive plant and by the Montana Natural Heritage Program as a Species of Concern in the state. This study, though attempting to be comprehensive, almost certainly has missed taxa that occur within the study area, and several small meadows and openings remain basically unsurveyed.

TABLE 1. SUMMARY OF TENDERFOOT CREEK EXPERIMENTAL FOREST FLORA.

Taxon	Families	Genera	Species
Ferns and fern allies	3	6	6
Pinophyta	2	5	9
Magnoliopsida	34	115	211
Liliopsida	5	36	86
Totals	44	162	312

TABLE 2. LARGEST FAMILIES OF TENDERFOOT CREEK EXPERIMENTAL FOREST FLORA.

Family	Species
Asteraceae	57
Poaceae	39
Cyperaceae	19
Rosaceae	16
Scrophulariaceae	16
Ericaceae	12

Floristic Affinities

The ecology and floristic diversity of an area may be better understood by looking at the floristic affinities of the species comprising the flora of the area in question. Insights into colonization events and migration patterns may also be gained by conducting analyses and summaries of floristic affinities. A species is considered to have an affinity with a particular floristic province when its distribution largely corresponds with that particular region (Gleason and Conquist 1964; Lesica 2002). TCEF itself sits near the boundary of two floristic provinces, the Cordilleran and the Great Plains (Grassland).

For the TCEF flora, we assigned species to the floristic provinces described by Gleason and Cronquist (1964). The flora of TCEF is dominated by species from two floristic provinces, the Boreal (Northern Conifer) and the Cordilleran. Approximately 47% of the species in the flora have a predominantly Cordilleran affinity and 25% have a Boreal affinity. This is not unexpected for an area such as TCEF, which occurs within the Cordilleran province at moderate to high elevations of the Northern Rocky Mountains and is dominated by subalpine conifer forests. Of the remaining species, the majority are widely distributed across two or more floristic regions and cannot be assigned to a specific province (18% are classified as widespread). Although elevations in the study area are not high enough to support an alpine life zone, a few meadows and exposed areas have conditions similar enough to alpine zones to support a few species from the Arctic-alpine province. Six species or roughly 2% of the flora fall into this category, including *Poa alpina* and *Sibbaldia*

TABLE 3. LARGEST GENERA OF TENDERFOOT CREEK EXPERIMENTAL FOREST FLORA.

Genera	Species
Carex	17
Poa	8
Salix	8
Juncus	7
Aster	6
Erigeron	6

procumbens. The remaining 8% of species are exotic to North America and do not fall into one of the floristic provinces. Many of the exotics were not collected during surveys in the 1990s but were observed in the 2003–2005 surveys, mainly along roads and in meadows adjacent to roads. Introductions of these species may be arising from increased human activity in the area. Currently, these exotics are a small component of the flora in terms of their area of extent and their contribution to floristic diversity. In comparison, the percent of the TCEF flora composed of exotics is slightly less but similar to the percent of exotics found in two other recent Montana floras from Flathead National Forest and Glacier National Park which cover larger and more diverse areas (Lesica 2002; Mantas 1999). No species with Great Plains affinities occur in TCEF probably because of the relatively high elevations of the study area. Species with Great Plains affinities do occur along the lower slopes of the Little Belt Mountains.

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Appendix I

Annotated Checklist

The checklist is arranged by division and class, then alphabetically by family and species. Nomenclature generally follows Dorn (1984). Common names are generally from Hitchcock and Cronquist (1973). Exotic species are preceded by an asterix (*). *Festuca rubra* and *Poa palustris* are preceded by double astrices (**) since their nativity is uncertain. Geographic abundance is included in the checklist using the following scale suggested by Palmer, Wade and Neal (1995):

Abundant—Dominant or codominant in one or more common habitats.

Frequent—Easily found in one or more common habitats, but not dominant in any common habitat.

Occasional—Widely scattered, but not difficult to find.

Infrequent—Difficult to find with few individuals or colonies, but found in several locations.

Rare—Very difficult to find and limited to one or very few locations.

In conjunction with an abundance category, the generalized habitats in which a species usually occurs are provided. Specific locations are provided for some species when they are only known to occur in one or two distinct areas. Collection numbers, listed at the end of each entry, are Scott Mincemoyer's unless otherwise

noted. Mincemoyer's collections are deposited at the MRC herbarium (Rocky Mountain Research Station, Forestry Sciences Laboratory, Missoula, MT) with some duplicates deposited at the MONT herbarium (Montana State University, Bozeman, MT). Taxa lacking collection numbers were identified by Scott Mincemoyer during field observations. Collections by Jennifer Birdsall are denoted by the initials JLB followed by a collection number and are on file at MRC. Collections by Earle Layser are distinquished by Layser followed by a collection number and are deposited at MONT. Collections by Jessica Fultz are distinquished by TCEF followed by a collection number and are deposited at MONT. Some additional specimens and duplicates are also included and are identified as such.

Division Equisetophyta

Equisetaceae

Equisetum arvense L. common horsetail. Infrequent. Wet meadows and streambanks. *245*.

Division Pterophyta

Polypodiaceae

Athyrium filix-femina (L.) Roth. Lady fern. Rare. Passionate Creek. *403*.

Cryptogramma acrostichoides R. Br. rock-brake. Rare. Rocky slopes. Quartzite Ridge.

Cystopteris fragilis (L.) Bernh. brittle bladder fern. Infrequent. Rocky slopes, crevasses and streambanks. *27, 65*.

Woodsia oregana D.C. Eaton. woodsia. Rare. Rocky slopes. *336*.

Selaginellaceae

Selaginella densa Rydb. selaginella. Rare. Open ridgetop above gravelpit. *296*.

Division Pinophyta

Cupressaceae

Juniperus communis L. common juniper. Occasional. Upland forests. *264*.

Juniperus scopulorum Sarg. Rocky Mtn. juniper. Rare. Steep, south slope near bottom of drainage. *337*.

Pinaceae

Abies lasiocarpa (Hook.) Nutt. subalpine fir. Abundant.

Picea engelmannii Parry. Engelmann spruce. Frequent. Most habitats except drier slopes.

Pinus albicaulis Engelm. whitebark pine. Frequent. Mature individuals at higher elevations and scattered seedlings and saplings elsewhere.

Pinus contorta Dougl. lodgepole pine. Abundant.

Pinus flexilis James. limber pine. Rare. Steep, south slope near bottom of drainage. *350*.

Pinus ponderosa Dougl. ponderosa pine. Rare. Steep, south slope near bottom of drainage. *349*.

Pseudotsuga menziesii (Mirbel) Franco. Douglas-fir. Rare. Scattered individuals in lower elevations.

Division Magnoliophyta

Class Magnoliopsida

Aceraceae

Acer glabrum Torr. Rocky Mountain maple. Rare. Lower portion of drainage. *251*.

Apiaceae

Angelica arguta Nutt. Lyall's angelica. Occasional. Streambanks with deep, rich soils.

Heracleum sphondylium L. cow-parsnip. Infrequent. Streambanks with deep, rich soils.

Lomatium cous (Wats) Coult. & Rose. cous biscuitroot. Infrequent. Dry Park and possibly in other dry meadows. *92, 278*.

Lomatium dissectum (Nutt.) Math. & Cronst. fern-leaved lomatium. Rare. Steep, south slope near bottom of drainage. *216*.

Lomatium triternatum (Pursh) Coult. & Rose. nine-leaf lomatium. Rare. Lower portion of drainage along roadside. *253*.

Osmorhiza chilensis H. & A. mountain sweet-cicely. Occasional. Moist forests. *106*.

Osmorhiza occidentalis (Nutt. Ex T. & G.) Torr. western sweet-cicely. Infrequent. Riparian forests. *271*.

Perideridia gairdneri (H. & A.) Mathias. Gairdner's yampah. Infrequent. Vernally moist meadows. *18*.

Apocynaceae

Apocynum androsaemifolium L. spreading dogbane. Rare. Steep, south slope near bottom of drainage. *344*.

Asteraceae

Achillea millefolium L. common yarrow. Occasional. Meadows and drier slopes. *301*.

Agoseris aurantiaca (Hook.) Greene. orange agoseris. Infrequent. Roadsides and drier meadows. *70, 118, 309*.

Agoseris glauca (Pursh) Raf. pale agoseris. Occasional. Meadows. *16, 42*.

Agoseris lackschewitzii Henderson & Mosely. pink agoseris. Rare. Wet meadows. Species described in Henderson et. al. (1990).

Anaphalis margaritacea (L.) B. & H. pearly everlasting. Occasional. Roadsides. *52*.

Antennaria anaphaloides Rydb. tall pussy-toes. Rare. Open ridgetop above gravelpit. *307*.

Antennaria corymbosa E. Nels. meadow pussy-toes. Rare. Wet meadows; Sun Creek area. *122*; *Layser 3289, 3337*.

Antennaria microphylla Rydb. rosy pussy-toes. Infrequent. Dry meadows. *305, 419* (*A. rosea* of some authors).

Antennaria parvifolia Nutt. Nuttall's pussy-toes. Rare. Open slope just west of Passionate Creek. *366* (MONT).

Antennaria racemosa Hook. woods pussey-toes. Frequent. Upland forests. *21; Clark 36*.

Arnica cordifolia Hook. heartleaf arnica. Infrequent. Upland forests, more common at lower elevations.

Arnica latifolia Bong. mountain arnica. Abundant. Upland forests and open slopes. *321*.

Arnica mollis Hook. hairy arnica. Infrequent. Wet meadows and streamsides. *Layser 3297*.

Arnica rydbergii Greene. Rydberg's arnica. Frequent. Upland forests; Sun Creek area. *TCEF 004* (MONT).

**Artemisia absinthium* L. wormwood. Infrequent. Roadsides. *JLB 25*.

Artemisia ludoviciana Nutt. gray sagewort. Rare. Steep, south slope near bottom of drainage. *348* (MRC, Dupl. MONT).

Aster ciliolatus Lindl. Lindley aster. Rare. Steep, south slope near bottom of drainage. *351*.

Aster conspicuus Lindl. showy aster. Infrequent. Tenderfoot Creek. *365*.

Aster foliaceus Lindl. leafy aster. Infrequent. Moist meadows and streamsides. *56.*

Aster hesperius Gray. western willow aster. Frequent. Stream banks and meadows; Sun Creek area. *TCEF 006* (MONT).

Aster integrifolius Nutt. thick-stemmed aster. Frequent. Dry meadows; Onion Park. *TCEF 008* (MONT).

Aster meritus A. Nels. arctic aster. Frequent. Open, upland forests. *81, 83, 127.*

Aster modestus Lindl. few-flowered aster. Rare. Lower portion of Tenderfoot Creek. *358.*

Aster occidentalis (Nutt.) T. & G. western aster. Frequent. Moist meadows and moist, open forests. *43, 75, 137, 313* (MONT), *327* (MONT); *Layser 3288, 3302.*

**Carduus nutans* L. musk thistle. Rare. Roadsides. *JLB 17.*

**Centaurea maculosa* Lam. spotted knapweed. Rare. Roadsides. *JLB 9.*

Chaenactis douglasii (Hook.) H. & A. hoary chaenactis. Rare. Lower portion of drainage along road.

**Chrysanthemum leucanthemum* L. oxeye-daisy. Infrequent. Roadsides. *JLB 6.*

**Cirsium arvense* (L.) Scop. Canada thistle. Infrequent. Roadsides and meadows.

Cirsium hookerianum Nutt. Hooker's thistle. Occasional. Meadows.

**Cirsium vulgare* (Savi) Tenore. bull thistle. Infrequent. Roadsides. *JLB 5.*

Crepis runcinata (James) T. & G. meadow hawksbeard. Rare. Dry Park. *423.*

Erigeron compositus Pursh. cutleaf daisy. Infrequent. Rocky slopes and outcrops in lower portion of drainage. *64, 266.*

Erigeron ochroleucus Nutt. buff fleabane. Rare. Open ridgetop above gravelpit. *297.*

Erigeron peregrinus (Pursh) Greene. Occasional. Onion Park area. *Clark 55.*

Erigeron simplex Greene. alpine daisy. Rare. Meadows. *132.*

Erigeron speciosus (Lindl.) DC. showy fleabane. Infrequent. Lower portion of drainage. *352* (MONT), *357* (MONT).

Erigeron ursinus DC. Eat. Bear River fleabane. Rare. Meadows; Stringer Creek area. *422.*

**Filago arvensis* L. filago. Rare. Along Road 586 west of Bubbling Springs. *401.*

Heterotheca villosa (Pursh) Shinners. hairy goldaster. Rare. Roadsides. *JLB 26.*

Hieracium albiflorum Hook. white-flowered hawkweed. Frequent. Upland forests. *367; Layser 3316.*

Hieracium cynoglossoides Arv.-Touv. hounds-tongue hawkweed. Infrequent. Open forests in lower portion of drainage. *361* (MRC, Dupl. MONT).

Hieracium gracile Hook. slender hawkweed. Frequent. Upland forests, more common with increasing elevation. *Layser 3317.*

**Lactuca serriola* L. prickly lettuce. Rare. Logged area. *JLB 27.*

Microseris nutans (Geyer ex. Hook.) Schultz-Bip. Rare. Dry meadows; Stringer Creek area. *420.*

Nothocalais nigrescens (Henderson) Heller. black-hairy nothocalais. Occasional. Dry meadows. *91.*

Senecio pseudaureus Rydb. streambank butterweed. Infrequent. Streamsides. *138; Layser 3284, 3308.*

Senecio sphaerocephalus Greene. mt-marsh butterweed. Infrequent. Meadows and roadsides. *79, 109; Layser 3282.*

Senecio triangularis Hook. arrowleaf groundsel. Frequent. Riparian forests, wet meadows and streamsides.

Solidago canadensis L. Canada goldenrod. Rare. Lower portion of Tenderfoot Creek. *405.*

Solidago missouriensis Nutt. Missouri goldenrod. Infrequent. Steep, south slope near bottom of drainage. *345* (MRC, Dupl MONT).

Solidago multiradiata Ait. northern goldenrod. Infrequent. Dry meadows and open slopes. *15, 316* (MONT).

**Sonchus arvensis* L. perennial sow-thistle. Rare. Roadsides. *JLB 27.*

**Tanacetum vulgare* L. common tansy. Rare. Roadsides. *JLB 16.*

**Taraxacum laevigatum* (Willd.) DC. red-seeded dandelion. Rare. Roadsides.

**Taraxacum officinale* Weber. common dandelion. Occasional. Meadows and roadsides.

**Tragopogon dubius* Scop. yellow salsify. Rare. Steep, south slope near bottom of drainage. *341.*

Berberidaceae

Mahonia repens (Lindl.) G. Don. creeping Oregon-grape. Infrequent. Forests and open areas in lower portion of drainage. *263.*

Betulaceae

Alnus viridis (Vill.) Lam. & DC. Sitka alder. Infrequent. Streamsides in lower portion of drainage. *247* (MRC, Dupl. MONT).

Boraginaceae

Mertensia ciliata (James ex. Torr.) G. Don. mountain bluebell. Occasional. Streamsides and wet meadows. *250.*

Mertensia oblongifolia (Nutt.) G. Don. leafy bluebells. Frequent. Meadows; Onion Park. *TCEF 002* (MONT).

Mertensia viridis (A. Nels.) A. Nels. green bluebells. Rare. Infrequent. Meadows; Onion Park area. *229.*

Brassicaceae

Arabis confinis Wats. spreading pod rockcress. Rare. Open areas in lower portion of drainage. *272* (MONT).

Arabis drummondii Gray. Drummond's rockcress. Infrequent. Meadows.

**Arabis glabra* (L.) Bernh. towermustard. Rare. Meadows; Onion Park area. *78.*

Arabis nuttallii Robins. Nuttall's rockcress. Occasional. Meadows and open slopes. *275.*

Barbarea orthoceras Ledeb. wintercress. Infrequent. Moist meadows and streamsides. *44.*

Cardamine breweri Wats. Brewer's bittercress. Infrequent. Wet meadows and streamsides. *Layser 3296, 3330.*

Draba stenoloba Ledeb. slender draba. Occasional. Open areas in meadows and along streams. *93.*

Rorippa curvisiliqua (Hook.) Bessey. western yellowcress. Rare. Vernally inundated depressions in meadows; one collection from small meadow east of Spring Park. *104.*

**Thlaspi arvense* L. field pennycress. Infrequent. Roadsides. *JLB 28.*

Thlaspi montanum L. Fendler's pennycress. Infrequent. Meadows. *31, 234.*

Campanulaceae

Campanula rotundifolia L. lady's thimble. Occasional. Meadows. *314*.

Caprifoliaceae

Linnaea borealis L. twinflower. Rare. Moist forests. *74*.
Lonicera utahensis Wats. Utah honeysuckle. Occasional. Forests and riparian areas.
Sambucus racemosa L. elderberry. Infrequent. Forests; heavily browsed by deer and elk. *244*.

Caryophyllaceae

Arenaria congesta Nutt. var. *lithophila* Rydb. ballhead sandwort. Infrequent. Rocky slopes. *53, 329* (MONT) (Hitchcock and Crounquist 1973).
Arenaria lateriflora L. Bluntleaf sandwort. Infrequent. Meadows; Onion Park area. *223*.
Cerastium arvense L. field chickweed. Infrequent. Meadows; Onion Park area. *141, 246*.
Silene parryi (Wats.) Hitchc. & Mag. Parry's silene. Infrequent. Dry meadows. *310* (MRC, Dupl. MONT).
**Spergularia rubra* (L.) J. & K. Presl. red sandspurry. Rare. Dry meadows and roadsides. *124*.
Stellaria crispa Cham. & Schlecht. crisped starwort. Rare. Moist depressions of forests. *58*.
Stellaria longifolia Muhl. ex Willd. long-leaved starwort. Infrequent. Meadows; Onion Park area. *Layser 3323*.
Stellaria sitchana Steud. northern starwort. Rare. Moist depressions of forests. *40*.

Crassulaceae

Sedum lanceolatum Torr. lanceleaf stonecrop. Rare. Dry meadows and rocky slopes. *277, 294*.

Ericaceae

Arctostaphylos uva-ursi (L.) Spreng. kinnikinnick. Infrequent. Dry, south-facing slopes. *364*.
Chimaphila umbellata (L.) Bart. prince's pine. Frequent. Upland forests.
Hypopitys monotropa Crantz. pinesap. Rare. Upland forests.
Ledum glandulosum Nutt. Labrador-tea. Rare. Wet meadows associated with *Sphagnum* spp.; upper portion of Sun Creek.
Pyrola asarifolia Michx. pink wintergreen. Rare. Moist forests; Onion Park area. *362; Layser 3287*.
Pyrola chlorantha Sw. green wintergreen. Occasional. Upland forests.
Pyrola minor L. lesser wintergreen. Rare. Forests. *133, 400* (MONT).
Pyrola secunda L. one-sided wintergreen. Occasional. Upland forests.
Vaccinium caespitosum Michx. dwarf huckleberry. Infrequent. Forests. *Layser 3299*.
Vaccinium globulare Rydb. globe huckleberry. Frequent. Moist forests; plants are diminutive in stature throughout TCEF. *242, 283, 368*.
Vaccinium myrtillus L. dwarf billberry. Abundant. Upland forests.
Vaccinium scoparium Leiberg. grouse whortleberry. Abundant. Upland forests.

Fabaceae

Astragalus alpinus L. alpine milkvetch. Occasional. Forest openings and rocky areas. *39, 240* (MONT), *421, 425* (MONT).
Astragalus bourgovii Gray. Bourgeau's milkvetch. Occassional. Meadows: gullies and along tree lines; Spring Park area. *TCEF 005* (MONT).
Hedysarum occidentale Greene. western hedysarum. Rare. Lower portion of Tenderfoot Creek. *252, 369*.
Lupinus argenteus Pursh. silvery lupine. Abundant. Forests.
**Medicago lupulina* L. black medic. Rare. Roadsides. *JLB 8*.
**Melilotus officinalis* (L.) Pallas. common yellow sweetclover. Rare. Disturbed site near flume in gravel. *JLB 20*.
Oxytropis cusickii Greenm. Rare. Open ridgetop above gravelpit. *276*.
**Trifolium hybridum* L. alsike clover. Occasional. Roadsides. *JLB 24*.
Trifolium longipes Nutt. long-stalked clover. Occasional. Moist meadows and forest openings. *233*.
**Trifolium pratense* L. red clover. Infrequent. Roadsides. *JLB 22*.
**Trifolium repens* L. white clover. Rare. Meadows and roadsides.

Gentianaceae

Frasera speciosa Dougl. giant frasera. Rare. Dry Park.
Gentiana affinis Griseb. pleated gentian. Rare. Moist meadows. *128; Layser 3324*.

Geraniaceae

Geranium bicknellii Britt. Bicknell's geranium. Rare. Dry meadows; Sun Creek and Onion Park. *TCEF 003* (MONT).
Geranium richardsonii Fisch. & Trautv. white geranium. Frequent. Moist to wet meadows and streamsides. *95, 261* (MONT).
Geranium viscosissimum F. & M. sticky geranium. Occasional. Meadows.

Grossulariaceae

Ribes lacustre (Pers.) Poir. black gooseberry. Occasional. Forests, rocky slopes and open areas along streams.
Ribes viscosissimum Pursh. sticky currant. Occasional. Rocky slopes and open areas along road paralleling Tenderfoot Creek. *262*.

Hydrophyllaceae

Phacelia hastata Dougl. silverleaf phacelia. Rare. Steep, south slope near bottom of drainage. *340*.
Phacelia sericea (Grah.) Gray. silky phacelia. Rare. Scree slope approx. ¾ mile SE of Dry Park and N of Road 839. *333* (MRC, Dupl. MONT).

Lamiaceae

Prunella vulgaris L. self-heal. Rare. Meadows and forest edges; west edge of Onion Park. *117*.

Onagraceae

Epilobium anagallidifolium Lam. alpine willow-herb. Infrequent. Wet meadows and streamsides. *112, 308* (MRC, Dupl. MONT); *Layser 3321, 3332*.
Epilobium angustifolium L. fireweed. Occasional. Roadsides and open forests.
Epilobium ciliatum Raf. common willow-herb. Frequent. Streamsides and wet meadows. *41; Layser 3322, 3327*.

Epilobium paniculatum Nutt. ex T. & G. tall annual willow-herb. Rare. Steep, south slope near bottom of drainage. *339.*

Plantaginaceae

Plantago major L. common plantain. Infrequent. Roadsides. *JLB 18.*

Polemoniaceae

Collomia linearis Nutt. narrow-leaf collomia. Occasional. Dry meadows and rocky slopes.

Phlox kelseyi Britt. var. *missoulensis* (Wherry) Cronq. Missoula phlox. Rare. Open ridgetop above gravelpit. 280; *Hitchcock & Muhlick 12311* (RM) (Hitchcock and Crounquist 1973).

Polemonium pulcherrimum Hook. skunk-leaved polemonium. Infrequent. Dry, open areas. *88.*

Polygonaceae

Eriogonum flavum Nutt. yellow buckwheat. Rare. Scree slope approx. ¾ mile SE of Dry Park and Nof Road 839. *328* (MONT).

Eriogonum umbellatum Torr. sulfur buckwheat. Rare. Open ridgetop above gravelpit. *298.*

Polygonum bistortoides Pursh. American bistort. Frequent. Wet meadows. *108, 225* (MONT).

**Polygonum convolvulus* L. black bindweed. Rare. Roadsides. *JLB 11.*

Polygonum douglasii Greene. Douglas's knotweed. Infrequent. Meadows and dry, open areas. *103, 302* (MONT); *Layser 3325.*

**Rumex acetosella* L. sheep sorrel. Infrequent. Roadsides. *JLB 19.*

Rumex paucifolius Nutt. mountain sorrel. Infrequent. Meadows; Onion Park. *317; Layser 3285; Clark 37.*

Portulaceae

Claytonia lanceolata Pursh. western springbeauty. Frequent. Forests at higher elevations. *94.*

Primulaceae

Androsace septentrionalis L. northern androsace. Infrequent. Barren areas along streams and in meadows. *101.*

Dodecatheon pulchellum (Raf.) Merrill. few-flowered shooting star. Frequent. Meadows. *84, 105, 226* (MONT), *274.*

Ranunculaceae

Actaea rubra (Ait.) Willd. baneberry. Rare. Shaded streambanks. *273.*

Delphinium bicolor Nutt. low larkspur. Rare. Meadows; Onion Park.

Ranunculus eschscholtzii Schlecht. subalpine buttercup. Rare. Rivulets in wet meadows; Onion Park. *236.*

Ranunculus inamoenus Greene. unlovely buttercup. Infrequent. Streamsides and wet meadows. *96, 418.*

Ranunculus uncinatus D. Don ex G. Don. little buttercup. Infrequent. Streamsides and wet meadows. *97.*

Thalictrum occidentale Gray. western meadowrue. Frequent. Moist forests. *232.*

Trollius laxus Salisb. American globeflower. Abundant. Openings of moist forests and wet meadows. *237.*

Rosaceae

Amelanchier alnifolia Nutt. serviceberry. Rare. Lower portion of drainage. *249.*

Fragaria virginiana Duchesne. blueleaf strawberry. Frequent. Forest openings, meadows and roadsides. *265.*

Geum macrophyllum Willd. large-leaved avens. Infrequent. Moist to wet meadows.

Geum rivale L. water avens. Rare. Moist to wet meadows; Onion Park. *TCEF 007* (MONT).

Geum triflorum Pursh. prairie smoke. Infrequent. Drier meadows; Onion and Dry Parks. *279.*

Potentilla diversifolia Lehm. diverse-leaved cinquefoil. Frequent. Meadows, moist forests and streamsides. *231.*

Potentilla glandulosa Lindl. sticky cinquefoil. Occasional. Rocky slopes along lower portion of Tenderfoot Creek. *63, 269.*

Potentilla gracilis Dougl. soft cinquefoil. Occasional. meadows and forest openings. *119.*

Prunus pensylvanica L. f. pin cherry. Rare. Steep, south slope near bottom of drainage. *343.*

Prunus virginiana L. common chokecherry. Rare. Steep, south slope near bottom of drainage. *342.*

Rosa acicularis Lindl. prickly rose. Infrequent. Lower portion of Tenderfoot Creek. *86, 254, 347* (MONT).

Rubus idaeus L. red raspberry. Occasional. Scree slopes and rocky areas; Quartzite Ridge.

Rubus parviflorus Nutt. thimbleberry. Rare. Passionate Creek. *402.*

Sibbaldia procumbens L. creeping sibbaldia. Infrequent. Roadsides and other exposed areas. *50.*

Sorbus scopulina Greene. Cascade mountain ash. Rare. Upland forests; one individual found on north slope. *59.*

Spiraea betulifolia Pall. shiny-leaf spirea. Frequent. Upland forests.

Rubiaceae

Galium boreale L. northern bedstraw. Occasional. Meadows and partially shaded streambanks. *24.*

Galium triflorum Michx. sweet-scented bedstraw. Rare. Moist areas in lower portion of drainage. *359* (MONT).

Salicaceae

Populus balsamifera L. spp. *trichocarpa* (Torr. & Gray. ex Hook.) Brayshaw. black cottonwood. Rare. One individual found along lower portion of Tenderfoot Creek. *215.*

Populus tremuloides Michx. quaking aspen. Infrequent. Lower portion of drainage on rocky slopes. *338.*

Salix barclayi Anderrs. Barclay's willow. Frequent. Streamsides and wet meadows along rivulets. *89, 113; Layser 3283, 3315.*

Salix bebbiana Sarg. Bebb willow. Rare. Lower portion of drainage. *255* (MRC, Dupl. MONT), *256.*

Salix boothii Dorn. Booth's willow. Occasional. Lower portion of drainage along Tenderfoot Creek. *243, 257, 376, 379* (MRC, Dupl. MONT).

Salix drummondiana Barratt. Drummond willow. Frequent. Streamsides and wet meadows along rivulets. *30, 377* (MONT); *Layser 3303, 3320.*

Salix geyeriana Anderss. Geyer's willow. Infrequent. Lower portion of drainage along Tenderfoot Creek. *388.*

Salix lasiandra Benth. Pacific willow. Rare. Lower portion of drainage along Tenderfoot Creek. *404.*

Salix melanopsis Nutt. Infrequent. dusky willow. Lower portion of drainage along Tenderfoot Creek. *389, 390.*

Salix scouleriana Barratt. Scouler willow. Occasional. Lower portion of drainage along Tenderfoot Creek and in forest openings. *378* (MONT), *387* (MRC, Dupl. MONT).

Saxifragaceae

Heuchera cylindrica Dougl. ex Hook. roundleaf alumroot. Occasional. Dry, rocky slopes. *346*.

Lithophragma glabrum Nutt. bulbiferous fringecup. Occasional. Wet meadows and streamsides. *107*.

Mitella pentandra Hook. alpine mitrewort. Occasional. Shaded streambanks. *130, 270* (MONT).

Mitella trifida Grah. Threeparted mitrewort. Rare. Moist forests. *424*.

Parnassia fimbriata Koenig. fringed grass of parnassus. Occasional. Streambanks and wet meadows. *25*.

Saxifraga occidentalis Wats. western saxifrage. Infrequent. Meadows; Onion Park. *100*.

Saxifraga odontoloma Piper. brook saxifrage. Occasional. Shaded streambanks.

Saxifraga oregana Howell. Oregon saxifrage. Occasional. Moist meadows. *230*.

Scrophulariaceae

Besseya wyomingensis (A. Nels.) Rydb. Wyoming besseya. Rare. Open ridgetop above gravelpit. *282*.

Castilleja cusickii Greenm. Cusick's paintbrush. Infrequent. Dry meadows; Dry Park and Onion Park. *29, 131; Layser 3298*.

Castilleja miniata Dougl. scarlet paintbrush. Occasional. Meadows and streambanks.

Collinsia parviflora Lindl. blue-eyed mary. Infrequent. Vernally moist slopes and meadows.

Mimulus guttatus DC. yellow monkey-flower. Rare. Streambanks.

Mimulus lewisii Pursh. Lewis' monkey-flower. Infrequent. Streambanks and partially shaded edges of wet meadows; primarily around Sun Creek.

Pedicularis bracteosa Benth. bracted lousewort. Infrequent. Upper elevation forests and wet meadows.

Pedicularis contorta Benth. white coiled-beak lousewort. Rare. Upper elevation forests.

Pedicularis groenlandica Retz. pink elephant's head. Infrequent. Wet meadows. *326*.

Pedicularis parryi Gray. Parry's lousewort. Rare. Open ridgetop above gravelpit. *281*.

Pedicularis racemosa Dougl. sickletop lousewort. Infrequent. Forests.

Penstemon attenuatus Dougl. var. *pseudoprocerus* (Rydb.) Cronq. small penstemon. Rare. Open slopes. *295, 399*. (Hitchcock and Crounquist 1973).

Penstemon procerus Dougl. ex Grah. small-flowered penstemon. Rare. Open slopes and meadows. *140*.

Veronica americana Schwein. American speedwell. Rare. Standing or flowing water; Sun Creek area. *36*.

Veronica serpyllifolia L. var. *humifusa* (Dickson) Vahl. thyme-leaved speedwell. Rare. Vernally inundated depressions in
meadows; one collection from small meadow east of Spring Park. *126*. (Hitchcock and Crounquist 1973).

Veronica wormskjoldii Roem. & Schult. alpine speedwell. Infrequent. Moist meadows.

Urticaceae

Urtica dioica L. stinging nettle. Rare. Open areas along streams; Stringer Creek.

Valerianaceae

Valeriana dioica L. northern valerian. Infrequent. Meadows. *111, 224* (MONT).

Valeriana sitchensis Bong. Sitka valerian. Frequent. Moist forests and meadows.

Violaceae

Viola macloskeyi Lloyd. small white violet. Rare. Streambanks and wet meadows. *98*.

Viola nuttallii Pursh. Nuttall's violet. Rare. Streambanks and wet meadows. *99*.

Viola orbiculata Geyer ex Holz. round-leaved violet. Abundant. Forests.

Class Liliopsida

Cyperaceae

Carex atrata L. blackened sedge. Infrequent. Wet meadows. *135*.

Carex canescens L. gray sedge. Rare. Wet meadows. *46*.

Carex concinnoides Mack. northwest sedge. Infrequent. Dry forests.

Carex disperma Dewey. soft-leaved sedge. Rare. Shaded streambanks and moist, forest edges. *125*.

Carex foenea Willd. dryspike sedge. Uncommon. Moist openings; lower portion of drainage. *374*.

Carex geyeri Boott. elk sedge. Abundant. Upland forests. *228*.

Carex hoodii Boott. Hood's sedge. Occasional. Moist openings; lower portion of drainage. *375*.

Carex lenticularis Michx. lakeshore sedge. Infrequent. Moist openings; lower portion of drainage. *73, 373*.

Carex microptera Mack. small-winged sedge. Frequent. Meadows. *23, 80, 85, 136, 318* (MONT), *320* (MONT).

Carex muricata L. muricate sedge. Infrequent. Wet meadows. *77*.

Carex norvegica Retz. Scandinavian sedge. Rare. Wet meadows; Onion Park. *Layser 3319*.

Carex phaeocephala Piper. dunhead sedge. Rare. SE of Dry Park just below scree slope. *330*.

Carex raynoldsii Dewey. Raynold's sedge. Occasional. Moist to wet meadows. *120, 300* (MRC & Dupl. MONT), *312* (MONT).

Carex rossii Boott. Ross' sedge. Infrequent. Forest openings. *258* (MRC, Dupl. MONT), *332* (MONT).

Carex scirpoidea Michx. var. *pseudoscirpoidea* (Rydb.) Cronq. single-spike sedge. Rare. Rocky slopes and meadows. *110, 304*.
(Hitchcock and Crounquist 1973).

Carex scopulorum Holm var. *prionophylla* (Holm) Standley. saw-leaved sedge. Infrequent. Wet meadows; Onion Park. *239, 372* (MRC, Dupl. MONT); *Layser 3290, 3310, 3311, 3340*.

Carex utriculata Boott beaked sedge. Occasional. Permanently saturated meadows and low gradient streams. *Layser 3291, 3309, 3335, 3336, 3339*. Incorrectly called *Carex rostrata* by Dorn (1984) and many other authors (Reznicek 1997).

Eriophorum chamissonis C. A. Mey. Chamisso's cotton-grass. Infrequent. Wet meadows, usually associated with *Sphagnum* spp.; Onion Park and Sun Creek areas. *4*; *Layser 3295, 3305, 3338*.

Eriophorum polystachion L. many-spiked cotton-grass. Rare. Wet meadows; Onion Park. *115*.

Juncaceae

Juncus balticus Willd. Baltic Rush. Occasional. Wet meadows. *38*.

Juncus confusus Cov. Colorado rush. Rare. Wet meadows. *68, 355* (MONT).

Juncus drummondii E. Meyer. Drummond's rush. Infrequent. Wet meadows. *22.*

Juncus ensifolius Wikst. dagger-leaf rush. Occasional. Wet meadows and streamsides. *360; Layser 3307.*

Juncus longistylis Torr. long-styled rush. Rare. Wet meadows; Sun Creek area. *76.*

Juncus mertensianus Bong. Merten's rush. Occasional. Wet meadows and streamsides. *Layser 3306.*

Juncus nevadensis Wats. Sierra rush. Infrequent. Wet meadows. *45.*

Luzula campestris (L.) DC. field woodrush. Infrequent. Moist meadows. *227* (MONT), *303* (MRC, Dupl. MONT).

Luzula parviflora (Ehrh.) Desv. small-flowered woodrush. Occasional. Shaded streambanks.

Liliaceae

Allium brevistylum Wats. short-styled onion. Occasional. Wet meadows; primarily Onion Park. *61.*

Allium cernuum Roth. nodding onion. Rare. Dry, open slopes. *306, 335* (MONT).

Allium geyeri Wats. Geyer's onion. Infrequent. Wet meadows; Onion Park. *102.*

Allium schoenoprasum L. chives. Occasional. Wet meadows; primarily Onion Park.

Camassia quamash (Pursh) Greene. common camas. Frequent. Wet meadows; primarily Onion Park.

Erythronium grandiflorum Pursh. glacier lily. Frequent. Upland, forests. *238.*

Fritillaria pudica (Pursh) Spreng. yellow bell. Infrequent. Meadows: along tree lines; Sun Creek and Onion Park. *TCEF 001* (MONT).

Smilacina stellata (L.) Desf. starry false Solomon's seal. Rare. Shaded streambanks and moist forests. *55.*

Streptopus amplexifolius (L.) DC. twisted-stalk. Rare. Shaded streambanks.

Veratrum viride Ait. green false hellebore. Frequent. Moist forest openings and wet meadows.

Zigadenus elegens Pursh. mountain death camas. Infrequent. Wet meadows and moist forest openings.

Orchidaceae

Calypso bulbosa (L.) Oakes. fairy-slipper. Rare. One individual found in moist forested bottom. *268.*

Corallorhiza maculata (Raf.) Raf. spotted coral-root. Rare. Moist forests.

Corallorhiza wisteriana Conrad. spring coral-root. Rare. One individual observed in a *Pinus contorta* forest.

Goodyera oblongifolia Raf. rattlesnake plantain. Occasional. Forests. *47, 363* (MONT).

Habenaria dilatata (Pursh) Hook. white bog orchid. Occasional. Wet meadows. *241; Layser 3292.*

Habenaria saccata Greene. slender bog orchid. Infrequent. Streambanks and wet meadows. *Layser 3293.*

Listera cordata (L.) R. Br. heart-leaf listera. Infrequent. Moist forests. *129, 267* (MONT).

Spiranthes romanzoffiana Cham. hooded ladies-tresses. Rare. Wet meadows; Onion Park. *116.*

Poaceae

Agrostis exarata Trin. spike bentgrass. Infrequent. Moist meadows. *37, 48* (MRC, Dupl. MONT); *Layser 3304, 3334.*

Agrostis idahoensis Nash. Idaho bentgrass. Rare. Moist meadows. *57; Layser 3312.*

Agrostis scabra Willd. tickle grass. Frequent. Meadows, roadsides and rocky slopes. *12; Layser 3286.*

Alopecurus alpinus Smith. alpine foxtail. Infrequent. Wet meadows; Onion Park. *114, 235* (MONT).

Bromus carinatus Hook. & Arn. California brome. Frequent. Meadows and moist, forest openings. *17; Layser 3313, 3318, 3328.*

Bromus ciliatus L. fringed brome. Infrequent. Moist, shaded to partially shaded forests. *14.*

**Bromus inermus* Leys. smooth brome. Occasional. Meadows and roadsides.

Calamagrostis canadensis (Michx.) Beauv. bluejoint reedgrass. Abundant. Moist forests and wet meadows. *371; Layser 3294, 3314.*

Calamagrostis purpurascens R. Br. purple reedgrass. Infrequent. Dry, rocky slopes. *324.*

Calamagrostis rubescens Buckl. pinegrass. Occasional. Upland forests, usually on drier slopes. *408.*

Cinna latifolia (Trevir.) Griseb. woodreed. Infrequent. Streambanks; lower portion of drainage. *396.*

**Dactylis glomerata* L. orchard-grass. Occasional. Roadsides, meadows and forest openings.

Danthonia intermedia Vasey. timber oatgrass. Frequent. Meadows and dry, rocky slopes. *11, 322* (MONT).

Deschampsia cespitosa (L.) Beauv. tufted hairgrass. Abundant. Moist to wet meadows. *60, 121, 139, 248* (MONT).

Deschampsia elongata (Hook.) Munro. slender hairgrass. Rare. Roadsides, along Road 586. *407.*

Elymus elymoides (Raf.) Swezey. bottlebrush squirreltail. Rare. SE of Dry Park just below scree slope. *334* (MRC, Dupl. MONT).

Elymus glaucus Buckl. blue wildrye. Frequent. Moist forests, wet meadows and streambanks. *32.*

Elymus spicatus (Pursh) Gould. bluebunch wheatgrass. Rare. Steep, south slope near bottom of drainage. *353.*

Elymus trachycaulus (Link) Gould ex Shinners. slender wheatgrass. Occasional. Moist to dry meadows. *13; Layser 3329.*

Festuca idahoensis Elmer. Idaho fescue. Infrequent. Dry meadows; Dry Park and Onion Park. *10, 325* (MONT).

***Festuca rubra* L. red fescue. Rare. Moist, open areas. *354.*

Festuca scabrella Torr. rough fescue. Infrequent. Dry meadows; Dry Park. *9.*

Glyceria elata (Nash ex Rydb.) Jones. tall managrass. Infrequent. Tenderfoot Creek. *356* (MRC, Dupl. MONT), *397* (MONT).

Koeleria macrantha (Ledeb.) Schultes. prairie junegrass. Rare. Open ridgetop above gravelpit. *311.*

Melica spectabilis Scribn. showy oniongrass. Frequent. Meadows and streambanks. *33.*

Phleum alpinum L. alpine timothy. Frequent. Meadows and moist, forest openings.

**Phleum pratense* L. timothy. Infrequent. Meadows and roadsides.

Poa alpina L. alpine bluegrass. Occasional. Meadows and forest openings. *69, 123, 142.*

Poa cusickii Vasey. Cusick's bluegrass. Infrequent. Meadows; Onion Park. *134.*

Poa interior Rydb. inland bluegrass. Infrequent. Open area along Tenderfoot Creek. *331* (MONT), *370.*

Poa leptocoma Trin. bog bluegrass. Infrequent. Wet meadows; Onion Park. *259; Layser 3331.*

Poa nervosa (Hook.) Vasey. Wheeler's bluegrass. Infrequent. Meadows and forest openings. *54, 260, 319* (MONT), *323* (MONT).

***Poa palustris* L. fowl bluegrass. Infrequent. Streambanks, lower portion of Tenderfoot Creek. *398* (MONT).

**Poa pratensis* L. Kentucky bluegrass. Infrequent. Roadsides and meadows. *51*.

Poa secunda Presl. Sandberg bluegrass. Rare. Open ridgetop above gravelpit. *299*.

Puccinellia pauciflora (Presl.) Munz. weak alkali grass. Infrequent. Standing or flowing water. *35*.

Stipa nelsonii Scribn. western needlegrass. Infrequent. Meadows and forest openings; Onion Park area. *315* (MRC, Dupl. MONT).

Trisetum spicatum (L.) Richter. downy oatgrass. Frequent. Meadows and dry, rocky slopes. *26*.

Trisetum wolfii Vasey. Wolf's trisetum. Occasional. Moist to wet meadows. *34, 49, 82; Layser 3326*.

Appendix II

Nonconfirmed Taxa

The following taxa have been reported for TCEF or Onion Park RNA by others but are not included in the main body of the flora since no voucher specimens were collected and some reported taxa are believed to be outside of the boundary of the experimental forest.

Apiaceae
Zizia aptera (Gray) Fern.
Asteraceae
Agoseris heterophylla (Nutt.) Greene
Cirsium scariosum Nutt.
Crepis elegans Hook.
Senecio dimorphophyllus Greene
Senecio pauperculus Michx.
Brassicaceae
Arabidopsis thalina L. Heynh.
Cardamine oligosperma Nutt.
Caprifoliaceae
Symphoricarpos albus (L.) Blake.
Caryophyllaceae
Silene douglasii Hook.
Stellaria crassifolia Ehrh.
Stellaria umbellata Turcz. ex Kar. & Kir.
Chenopodiaceae
Chenopodium album L.
Crassulaceae
Sedum stenopetalum Pursh.
Cyperaceae
Carex aurea Nutt.
Carex pellita Muhl. ex Willd.
Carex praegracilis W. Boott
Eleocharis pauciflora (Lightf.) Link
Elaeagnaceae
Shepherdia canadensis (L.) Nutt.
Equisetaceae
Equisetum palustre L.
Gentianaceae
Gentiana calycosa Griseb.
Liliaceae
Xerophyllum tenax (Pursh) Nutt.
Orchidaceae
Habenaria hyperborea (L.) R. Br.
Habenaria viridis (L.) R. Br.
Poaceae
Bromus vulgaris (Hook.) Shear
Polemoniaceae
Linanthus nuttallii (Gray) Greene ex Milliken
Linanthus septentrionalis Mason
Polygonaceae
Polygonum viviparum L.
Ranunculaceae
Anemone multifida Poir.
Ranunculus macounii Britt.
Salicaceae
Salix farriae Ball.
Salix lutea Nutt.
Saxifragaceae
Lithophragma parviflora (Hook.) Nutt. ex Torr. & Gray
Mitella breweri Gray.
Scrophulariaceae
Castilleja occidentalis Torr.
Veronica cusickii Gray
Solanaceae
Hyoscyamus niger L.

Appendix III

Synonyms And Excluded Names

Boraginaceae
Mertensia lanceolata (Pursh) DC. Synonymous with *Mertensia viridis* (A. Nels.) A. Nels.
Onagraceae
Epilobium halleanum Hausskn. Included under *Epilobium ciliatum* Raf.
Epilobium lactiflorum Hausskn. Included under *Epilobium anagallidifolium* Lam.
Salicaceae
Salix monticola Bebb. Name misapplied: specimens belong to *Salix barclayi* Anderrs.

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SYSTEMATIC RELATIONSHIPS OF SARRACENIACEAE INFERRED FROM NUCLEAR RIBOSOMAL DNA SEQUENCES

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ABSTRACT

The Sarraceniaceae are a small family of insectivorous herbs native to North and South America. The family is composed of three geographically separated genera, *Heliamphora, Darlingtonia* and *Sarracenia*. Recent molecular evidence suggests that *Darlingtonia* is sister to a *Heliamphora-Sarracenia* clade. The systematic relationships among the taxa within the genus *Sarracenia* are uncertain. Within the *S. rubra* and *S. purpurea* complexes, five and four infraspecific taxa have been named respectively. In this study, combined Internally Transcribed Spacer 2 and 26S large ribosomal subunit rRNA gene DNA sequences were used to infer phylogenetic relationships among the genera within Sarraceniaceae and the specific and subspecific taxa within *Sarracenia*. Results from this study support the sister relationship between *Darlingtonia* and a *Sarracenia-Heliamphora* clade. Within the genus *Sarracenia, S. purpurea* is sister to all remaining species. Additionally, the four named infraspecific taxa of *S. purpurea* are resolved in a well-supported clade. However, the five named subspecific taxa of *S. rubra* are part of a polytomy without discernable structure. This study suggests that *S. purpurea* ssp. *purpurea* var. *burkii* (which has been named a separate species as *S. rosea*) may be considered a distinct species. If so treated, then the number of species of *Sarracenia* stands at nine.

Key Words: Darlingtonia, Sarracenia, Heliamphora.

The Sarraceniaceae are a small family of insectivorous herbs native to North and South America. The family is composed of three geographically separated genera. *Heliamphora* consists of about six species and occurs in Venezuela and British Guiana (Lloyd 1942; DeBuhr 1975; Maguire 1970, 1978). The eight or so species of *Sarracenia* occur in the southeastern US (Lloyd 1942; McDaniel 1966; DeBuhr 1975) with one, *S. purpurea*, ranging as far north as Canada (Maguire 1970). The monotypic *Darlingtonia* occurs in northern California and western Oregon (Lloyd 1942; DeBuhr 1975).

Infrafamilial Relationships

Several hypotheses concerning the infrafamilial relationships of *Sarraeniaceae* have been offered. Croizat (1960) suggested that the ancestor to Sarraceniaceae may have arrived in South America via Africa. His hypothesis is consistent with positioning the South American *Heliamphora* as sister to a *Sarracenia-Darlingtonia* clade. McDaniel (1966) suggested that the ancestral Sarraceniaceae had begun migrations into their present locations during the pre-Cretaceous. In support of his hypothesis, McDaniel (1966) noted that *Sarracenia* and *Heliamphora* occur in areas known for their endemism and antiquity (i.e., Southern Appalachians and Guyana Highlands) respectively.

Thanikaimoni and Vasanthy (1972) performed a palynological study of the Sarraceniaceae and determined that *Heliamphora* has 3-colporate pollen, whereas *Sarracenia* has 9-colporate pollen. Thanikaimoni and Vasanthy (1972) stated that if this character has phylogenetic value, then this finding suggests that *Heliamphora* is more primitive than *Sarracenia*.

Maguire (1978) suggested that the profound morphological distinctions among the three genera indicate an ancient independent history for each genus in the family. He further suggested that morphological characters suggest that *Heliamphora* is closest to any ancestral prototype and that the origin of this ancestor was in the Guyana Highlands of South America.

Mellichamp (1983) posited that ancestral pitcher plants evolved approximately 40–60 MYA in what is now the southeastern United States. At that time, the climate was favorable to pitcher plants and may have allowed *Darlingtonia* or its ancestors to migrate across the continent to the west coast before the rise of the Sierras and the Rocky Mountains, and allowed *Heliamphora* to migrate to South America (Mellichamp 1983).

According to Renner (1989), *Sarracenia* and *Heliamphora* probably arose from ancestral stock that was widespread and adapted to acidic bogs.

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During severe climactic change (such as that which occurred in the Pleistocene) these bog habitats were largely lost. The remaining bog habitats were isolated and the surviving plants there became specialized in their floral biology (Renner 1989).

Results from a phylogenetic analysis based on chloroplast *rbc*L sequences by Albert et al. (1992) suggested that the African taxon *Roridula* (Roridulaceae) is sister to Sarraceniaceae. That study also indicated that *Darlingtonia* is sister to a *Heliamphora-Sarracenia* clade. Albert et al.'s (1992) phylogeny is supported by the molecular-based study by Bayer et al. (1996) in which both *rbc*L and Internally Transcribed Spacer (ITS) 1 and 2 DNA sequences were combined in one analysis. That study also found that *Roridula* is sister to Sarraceniaceae and that *Darlingtonia* is sister to a *Heliamphora-Sarracenia* clade.

Infrageneric Relationships of *Sarracenia*

The systematic relationships within the genus *Sarracenia* are uncertain and there is no consensus on the number of species within the genus. In a taxonomic revision of *Sarracenia*, McDaniel (1966) reported a characteristic pattern of flavonoids for each species of *Sarracenia*. However, he concluded that these data provided little evidence of phylogenetic relationships.

Schnell and Krider (1976) performed a phenetic analysis of the genus using 19 traditional (non-molecular) characters. The dendrogram produced from that analysis consisted of four main operational taxonomic unit clusters. However, such an analysis, based on overall similarity, cannot be used to infer phylogenetic relationships.

An analysis by Romeo et al. (1977) concluded that the flavonoid components of all *Sarracenia* species are remarkably similar. However, they noted that a consistent lack of certain components in the "rubra-complex" (*sensu* Case and Case 1976) suggested that this closely related group may be derived within the genus. Additionally, they noted that the northern populations of *S. purpurea* but not the southern populations lack these same two components. Romeo et al. (1977) attributed this difference to the recent availability of northern habitats for *S. purpurea*. In contrast to the findings by McDaniel (1966), Romeo et al. (1977) found no characteristic pattern of flavonoids for each species of *Sarracenia*.

Schnell (1978) performed a chromatographic study of petal extract of *Sarracenia*. Although he discussed possible phylogenetic relationships among the representatives sampled, Schnell (1978) concluded that those data are of limited value in that regard. Finally, the study based on combined ITS 1 and 2 DNA sequences by Bayer et al. (1996) recovered trees with little resolution and poor bootstrap support with respect to relationships of *Sarracenia*.

Infraspecific Relationships of *Sarracenia rubra*

Much discussion concerning the variants of *Sarracenia rubra* is present in the literature. For example, McDaniel (1966) noted that *S. rubra* occurs in isolated areas from Mississippi to North Carolina and that various populations of this species may have been separated for longer periods than disjunct populations of other species of *Sarracenia*. McDaniel (1966) further noted that mountain populations are morphologically different but connected by intermediates to sandhill area populations. Individuals from the outer coastal plain of the Carolinas and from west Florida to Mississippi are the most diverged (McDaniel 1966). Later, McDaniel (1971) stated that *Sarracenia rubra* has four morphological forms that are correlated with geographical distribution. McDaniel (1971) noted that intergradation between these forms is common and that the naming of infraspecific taxa is not warranted.

However, other authors have recognized and named variants of *S. rubra*. For example, Wherry (1929) named the disjunct mountain variant as the new species *S. jonesii* but subsequently reduced its rank to *S. rubra* ssp. *jonesii* (Wherry 1933). Case and Case (1974) named the central Alabama disjunct as the new species *Sarracenia alabamensis*.

The naming of variants of *S. rubra* is supported by a morphology-based phenetic analysis of *Sarracenia* by Schnell and Krider (1976). In that study, the authors concluded that the degree of dissimilarity among the mountain, Gulf Coast and eastern Carolina populations would indicate that some infraspecific taxonomic separation may be warranted.

Schnell (1977) stated that there is insufficient discontinuity of characters among the variants of *S. rubra* to consider any as distinct species. However, he did note that as many as five subspecies may be recognized. Therefore, Schnell (1977) reduced the rank of *S. alabamensis* to *S. rubra* ssp. *alabamensis* and named the populations from southern Alabama as *S. rubra* ssp. *wherryi*. Later, Schnell (1979a) named the populations from northwest Florida as *S. rubra* ssp. *gulfensis*.

The molecular-based study by Bayer et al. (1996) failed to resolve the relationship between two *S, rubra* variants they termed S. *rubra* and S. *jonesii*.

Infraspecific Relationships of *Sarracenia purpurea*

Much literature also has been devoted to the variants of *S. purpurea*. Rafinesque (1840) recognized two morphologically and geographically

distinct taxa. The long, glabrous-leaved northern species, occurring from Canada to Virginia, was named *Sarazina* (=*Sarracenia*) *gibbosa* and the short, pubescent variant, occurring from Virginia to Florida, was named *Sarazina venosa*. Rafinesque (1840) also recognized *Sarazina heterophylla* from New England. Wherry (1933) renamed and reduced the rank of Rafinesque's (1840) northern species to *Sarracenia purpurea* ssp. *gibbosa* and the southern species to *S. purpurea* ssp. *purpurea*. Because the ranges of the two subspecies overlap and intergradation occurs in southern New Jersey (Wherry 1933), Wherry (1973) reaffirmed segregating the two variants into subspecies (rather than species). Godt and Hamrick (1998), however, reported that the ranges of the two subspecies overlap in Maryland and Delaware; according to Kartesz and Meacham (1999) both subspecies occur in Delaware, New Jersey and Virginia.

The flavonoid- and amino acid-based study of Romeo et al. (1977) suggested a distinction between the northern and southern populations of *S. purpurea*. Specifically, although they found that the major flavonoid components of all *Sarracenia* species were remarkably similar, they noted that two flavonoid components were absent in the northern populations of *S. purpurea* whereas, they were present in the southern populations.

A petal extract chromotography study by Schnell (1978) failed to find a material distinction between the two subspecies of *Sarracenia purpurea*. However, due to the limitations of this technique in *Sarracenia*, Schnell (1978) suggested that his results did not necessarily discount the recognition of subspecific status for each.

Schnell (1979b) noted that clinal, genetic and phenotypic variations are to be expected in populations of *S. purpurea* due to its extensive range. Although he cautiously accepted the two subspecies named by Wherry (1933), he thought there was little basis for the naming of variants within *S. purpurea* ssp. *venosa*. However, Schnell (1979b) mentioned that additional research may warrant the naming of a new variety for the Gulf Coast populations. Later, Schnell (1993) named the Gulf Coast populations *S. purpurea* ssp. *venosa* var. *burkii*. based on an analysis of morphological characters. Naczi et al. (1999) elevated this taxon to specific status as *S. rosea*. Schnell and Determann (1997) recognized another southern variant native to the mountains and Piedmont of Georgia and North Carolina and named it *S. purpurea* ssp. *venosa* var. *montana*.

In their phenetic analysis, Godt and Hamrick (1998) reported that their most striking observation is the high level of allozyme divergence found among *S. purpurea* populations. They stated that 90% of this divergence is due to differences between infraspecific taxa and suggested that this divergence is due primarily to restricted gene exchange for a considerable period of time. Their phenogram indicates that the Gulf Coast populations (var. *burkii*) are the most distinct, that the Atlantic Coast populations (var. *venosa*) are most closely allied with the mountain populations (var. *montana*) followed by the northern populations (ssp. *purpurea*).

In contrast to the high level of allozyme divergence found in the *S. purpurea* species complex, Godt and Hamrick (1998) reported that there is little genetic differentiation among disjunct subspecies of the *S. rubra* complex. This suggests that the *S. rubra* subspecies diverged rather recently or that levels of gene flow between them have been high (Godt and Hamrick 1998).

Ellison et al. (2004) reported that morphological variation in *Sarracenia purpurea* is associated with environmental factors and geography. Specifically, they indicated that the size and shape of pitchers are primarily a function of precipitation, temperature and latitude. Ellison et al. (2004) reported that there is no obvious way to distinguish the two subspecies of *S. purpurea* by morphology and that this supports Gleason and Cronquist (1991) in that the two subspecies are merely geographical variants. However, Ellison et al. (2004) claimed that their data do support the differentiation of the Gulf Coast populations.

The goal of this study is to develop a molecular-based phylogeny of the Sarraceniaceae with primary interest on the genus *Sarracenia*. This phylogeny, will be inferred from combined nuclear-encoded ITS2 and 26S large ribosomal subunit rRNA gene sequences. A well-supported phylogeny will provide additional insight into the evolutionary patterns and relationships that will serve as a basis for comparison with previous studies.

METHODS

Vouchers and GenBank accessions for the taxa included in this study are listed in Table 1. The ingroup consists of representatives from *Sarracenia, Heliamphora*, and *Darlingtonia* (Table 1). *Roridula* was selected as outgroup following Albert et al. (1992) and Bayer et al. (1996). All taxa included in *Sarracenia* (*sensu* Kartesz and Meacham 1999) are included. This includes all subspecific taxa within the *S. rubra* and *S. purpurea* complexes. Note that Kartesz and Meacham (1999) include southern populations of *S. purpurea* in ssp. *purpurea* (not ssp. *venosa*) and northern populations in ssp. *gibbosa*.

For enhanced context, multiple representatives of *Sarracenia alata* and *S. leucophylla* are included. Although the range of *S. alata* is separated into an eastern and western disjunct (Sheridan 1991), no infraspecific taxa have been named. Three representatives from each disjunct

TABLE 1. TAXA ANALYZED IN THIS STUDY. All ingroup representatives are from Sarraceniaceae with *Roridula dentata* (Roridulaceae) as outgroup. All sequences have been deposited in GenBank. Vouchers are housed at the McNeese State University herbarium (MCN). Location data for wild-collected specimens are indicated. Taxonomy follows Kartesz and Meacham (1999). Representatives of *Sarracenia alata* from the eastern and western disjuncts are designated.

Taxon	Voucher	GenBank accession
Sarracenia alata Wood (Western Disjunct)	Neyland 1496 Calcasieu Parish, LA	AY795884
Sarracenia alata Wood (Eastern Disjunct)	Neyland 2112 Jackson County, MS	AY789969
Sarracenia alata Wood (Eastern Disjunct)	Neyland 2120 Tangipahoa Parish, LA	AY789968
Sarracenia alata Wood (Eastern Disjunct)	Neyland 2108 Stone County, MS	AY795883
Sarracenia alata Wood (Western Disjunct)	Neyland 2122 Hardin County, TX	AY796054
Sarracenia alata Wood (Western Disjunct)	Neyland 2123 Natchitoches Parish, LA	AY795885
Sarracenia flava L.	Neyland 2109 Santa Rosa County, FL	DQ017391
Sarracenia leucophylla Raf.	Neyland 2113 Jackson County, MS	AY796055
Sarracenia leucophylla Raf.	Neyland 2110 Santa Rosa County, FL	DQ088065
Sarracenia leucophylla Raf.	Neyland 2117 Baldwin County, AL	DQ088066
Sarracenia minor Walt.	Neyland 2139	DQ073470
Sarracenia oreophila (Kearney) Wherry	Neyland 2131	AY950690
Sarracenia psittacina Michx.	Neyland 2121 Tangipahoa Parish, LA	AY967802
Sarracenia purpurea L. ssp. *gibbosa* (Raf.) Wherry	Neyland 2137	DQ028630
Sarracenia purpurea L. ssp. *purpurea* var. *burkii* Schnell	Neyland 2142 Escambia County, FL	DQ088067
Sarracenia purpurea L. ssp. *purpurea* var. *montana* Schnell & Determann	Neyland 2136 Henderson County, NC	DQ028631
Sarracenia purpurea L. ssp. *purpurea* var. *purpurea*	Neyland 2154	DQ098117
Sarracenia rubra Walt. ssp. *alabamensis* (F.W. & R.B. Case) Schnell	Neyland 2129	AY942694
Sarracenia rubra Walt. ssp. *gulfensis* Schnell	Neyland 2141	DQ076326
Sarracenia rubra Walt. ssp. *jonesii* (Wherry) Wherry	Neyland 2130 Henderson County, NC	DQ017392
Sarracenia rubra Walt. ssp *rubra*	Neyland 2135	DQ028629
Sarracenia rubra Walt. ssp. *wherryi* (F.W. & R.B. Case) Schnell	Neyland 2153	DQ076326
Darlingtonia californica Torr.	Neyland 2133	DQ017390
Heliamphora heterodoxa Steyerm.	Neyland 1809	AY796056
Roridula dentata L	Neyland 2128	AY950689

were included in this analysis. The recovered systematic patterns among the disjunct representatives of *S. alata* are compared with those among the disjunct representatives of both *S. rubra* and *S. purpurea*.

The range of *S. leucophylla* is continuous and no infraspecific taxa have been named. Three representatives from different populations of *S. leucophylla* were also included in this analysis. The recovered systematic patterns among these three *S. leucophylla* representatives are, likewise, compared with those among the disjunct representatives of *S. rubra, S. purpurea*, and *S. alata*.

When possible, DNA was extracted from the leaves of plants in natural populations. However, in some cases, leaves from greenhouse maintained individuals were used. Collection details for samples are referenced in Table 1.

An approximate 1kb DNA segment of the 26S gene and an approximate 245 base-pair length nuclear ribosomal ITS2 region for each representative listed in Table 1 was analyzed in this study. Because Bayer et al. (1996) used ITS sequences with limited success, the 26S segment was sequenced to augment the amount of data for this analysis. The ITS2 and 26S segments are contiguous in the nuclear genome. The 26S fragment which spans base positions 1–958 in *Nicotiana tabacum* (GenBank Accession AF479172) is characterized by conserved segments and more variable expansion segments designated as D2, D3, and D4 by Kuzoff et al. (1998). Most of the variability within this gene is found in the first kb (Kuzoff et al. 1998). The rate of divergence in this 26S segment has been shown to be informative at the specific and infraspecific level in studies of the family Ericaceae which is closely related to Sarraceniaceae (e.g., Neyland 2004; Neyland and Hennigan 2004).

DNA sequences were used to infer systematic relationships of *Sarraceniaceae* through a maximum parsimony phylogenetic analysis using the heuristic search algorithm with Phylogenetic Analysis Using Parsimony (PAUP version 4.0b10) software (Swofford 2002). Searches employed 1000 random stepwise addition replications. All characters including transitions and transversions were weighted equally. Gaps were treated as missing data. Disk copies of aligned sequences are available from the author. As a measure of clade stability or robustness, bootstrap support (Felsenstein 1985) was calculated. Ten thousand bootstrap replications were employed in this analysis (MulTrees option in effect).

Total DNA was extracted from tissue using the CTAB method of Doyle and Doyle (1987). DNA sequences were amplified via polymerase chain reaction (PCR) (Mullis and Faloona 1987) with combinations of forward and reverse primers referenced in Neyland (2002).

DNA was amplified with Tfl enzyme (Epicentre Technologies, Madison, WI), using the following thermocycling protocol: a hot start at 94°C for 3 min; 30 amplification cycles of 94°C for 1 min, 55°C for 1 min; 72°C for 3.5 min, a terminal extension phase at 72°C and an indefinite terminal hold at 4°C. The double-stranded PCR product was purified with QIAquick (Qiagen, Hilden, Germany) using the manufacturer's protocol. Two µl of each sample was electrophoresed in a 1.0% agarose mini-gel for quantification against a known standard. Automated sequencing was conducted on an ABI Prism 377 Sequencer with XL Upgrade (housed at Louisiana State University, Baton Rouge, LA, USA) using ABI Prism, Big Dye Terminator cycle sequencing protocol (P.E. Applied Biosystems, Foster City, CA, USA). Sequences have been deposited in the GenBank database (Table 1).

Results

Sequences were aligned by visual inspection. Gaps were introduced to accommodate 29 single-point insertions/deletions (INDELS) in the data set. Nineteen gaps were inserted in the ITS2 segment and 10 gaps were inserted in the 26S segment. INDELS were not treated as characters. The largest absolute distance between any two members in the data set was 134 between *Roridula dentata* and *Sarracenia minor*. The smallest absolute distance between any two members in the data set was 0 between *Sarracenia alata* (2108) and *S. alata* (2112); *S. alata* (2123) and *S. alata* (2122); *S. leucophylla* (2110) and *S. leucophylla* (2117); *S. rubra* ssp. *wherryi* and *S. oreophila; S. rubra* ssp. *jonesii* and *S. oreophila*. Unambiguous transitions and transversions numbered 116 and 43 respectively. Therefore, transitions outnumbered transversions by a factor of about 3 to 1. Phylogenetic analiysis resulted in the recovery of 51 most-parsimonious trees. Each tree was 279 steps with a consistency index of 0.9068 and a retention index of 0.8497.

Systematic Relationships of Sarraceniaceae

As depicted in the cladograms, *Darlingtonia* is sister to a *Heliamphora-Sarracenia* clade (Figs. 1, 2). This branching pattern is consistent with the molecular-based phylogenies recovered by Albert et al. (1992) and Bayer et al. (1996). The place of origin for the ancestral Sarraceniaceae is equivocal.

Systematic Relationships of *Sarracenia*

The recovered topology strongly supports the position of *Sarracenia purpurea* as sister to the remaining species of the genus (Figs. 1, 2). This position is contrary to that suggested by Bayer et al.'s (1996) study that indicated that *S. alata* is sister to all other species in the family and that *S. purpurea* is sister to *S. leucophylla*. However, the branches that depicted those relationships in Bayer et al.'s (1996) study received less than 50% bootstrap support. Additionally, the findings of the present study do not support the cluster composed of *S. purpurea, S. leucophylla*, and *S. psittacina* recovered by Schnell and Krider's (1976) phenetic analysis.

All four named infraspecific taxa within *Sarracenia purpurea* were resolved (Figs. 1, 2). Absolute nucleotide pair-wise differences among these taxa range from 4 to 10. The cladistic relationships among these taxa in this study match the distance relationships reported by Godt and Hamrick (1998). The branching pattern in this clade depicts *S. purpurea* ssp. *purpurea* var. *burkii* as sister to the remaining infraspecific taxa.

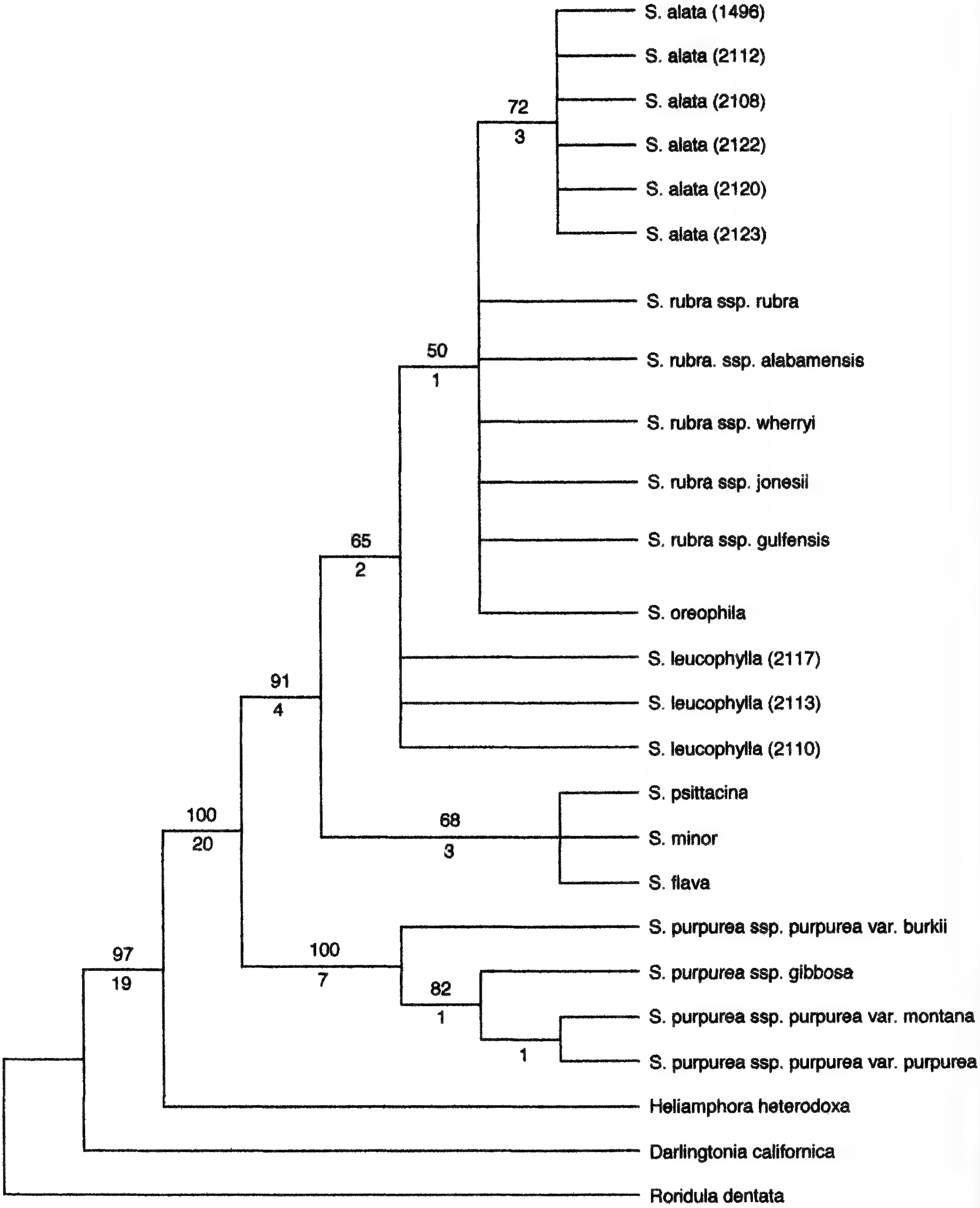

FIG. 1. Strict consensus tree recovered from a maximum parsimony heuristic search. Bootstrap values greater than 50% are indicated above each branch. Unequivocal synapomorphies are indicated below each branch. Voucher numbers for taxa with multiple representatives are indicated.

Therefore, the recovered topology suggests that *S. purpurea* ssp. *purpurea* is polyphyletic. Furthermore, the strongly supported dichotomy between *S. purpurea* ssp. *purpurea* var. *burkii* and the other infraspecific *S. purpurea* supports Naczi et al.'s (1999) elevation of this taxon to specific status as *Sarracenia rosea*.

The recovered topology suggested a moderately supported clade composed of *Sarracenia flava, S. minor*, and *S. psittacina* (Figs. 1, 2). This same

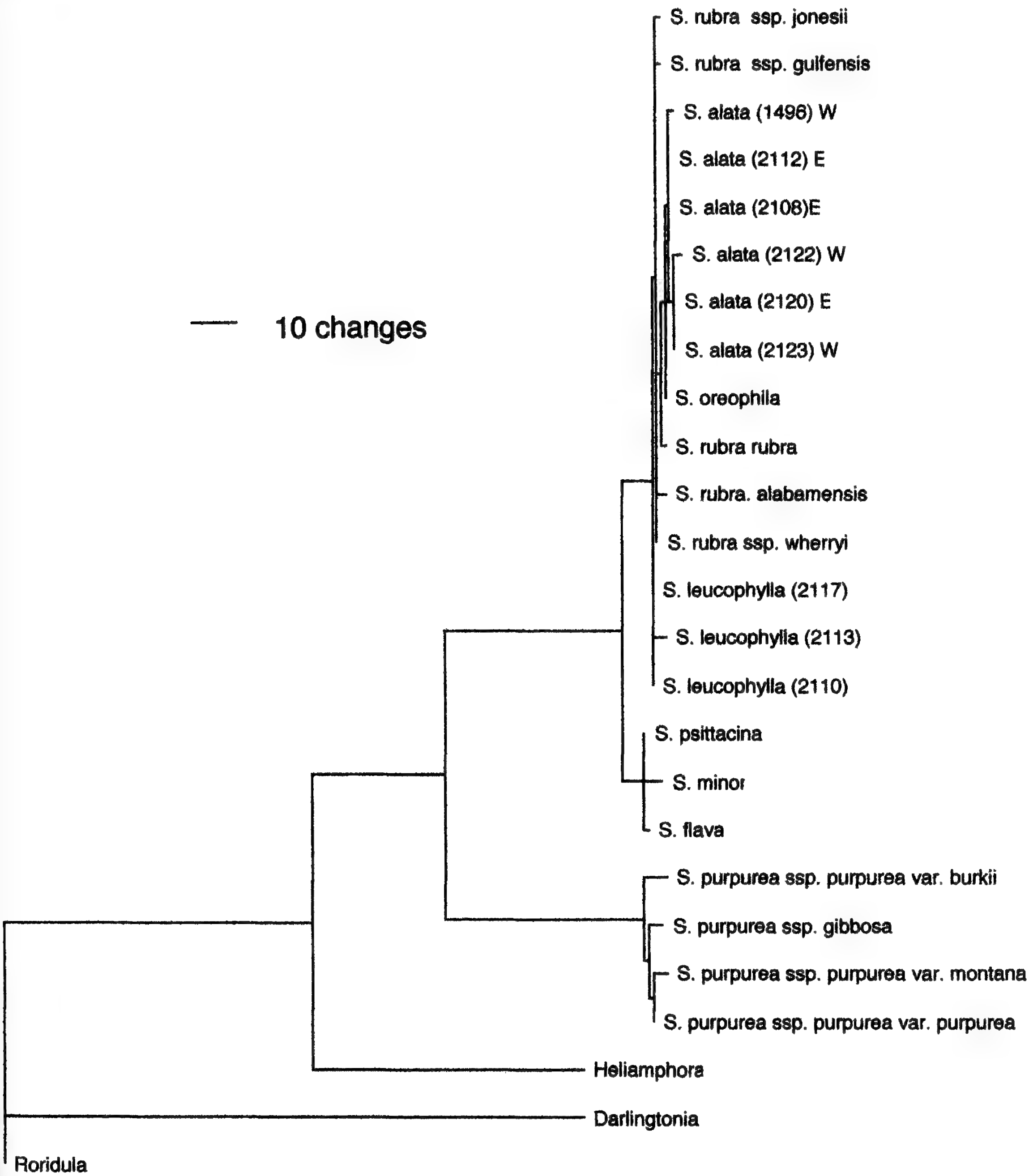

FIG. 2. Phylogram of one of the 51 most-parsimonious trees recovered in the maximum parsimony heuristic search. The changes legend indicates branch length.

clade was recovered in Bayer et al.'s (1996) analysis and was the only clade within *Sarracenia* that received greater than 50% bootstrap support in that study.

The polytomy consisting of *Sarracenia oreophila*, six representatives of *S. alata* and the five subspecies of *S. rubra* was moderately supported and suggests a close affinity among these three species. Because there were no more than two absolute nucleotide differences between any two representatives, the subspecies of *S. rubra* appeared to be very closely related.

Although the eastern and western disjuncts of *Sarracenia alata* are separated by over 300 km at their closest point, the recovered topology suggests no discernable phylogenetic structure between the two (Figs. 1, 2). No more than three absolute nucleotide differences between the se-

quences of any two representatives were evident in the data. The derived position of *S. alata* contrasts with its basal position recovered in the topology by Bayer et al. (1996). However, as previously stated, the branch supporting the position of *S. alata* in the Bayer et al. (1996) study received less than 50% bootstrap support. The close affinity between *S. alata* and *S, rubra* has been suggested previously (McDaniel 1966; Schnell and Krider 1976).

Sarracenia oreophila also appeared in the derived polytomy with *S. rubra* and *S. alata*. Absolute nucleotide pair-wise differences between *S. oreophila* and the representatives from *S. rubra* and *S. alata* ranged between 0 and 2. An affinity between *S. oreophila* and S. *alata* has been suggested (McDaniel 1966; Schnell 1979b) and an affinity between *S. oreophila* and *S. rubra* has been suggested (McDaniel 1966; Case and Case 1976). However, *S. oreophila* clustered with *S. flava* in the phenetic study of Schnell and Krider (1976) and its position was unresolved in Bayer et al.'s (1996) study. The derived polytomy consisting of *S. alata, S. rubra* and *S. oreophila* suggests that these taxa are closely related, have evolved relatively recently, and have radiated rapidly.

The three representatives of *Sarracenia leucophylla* appeared in the cladogram as sister to the polytomy that includes *S. alata, S. oreophila*, and *S. rubra*. Absolute nucleotide differences among the representatives of *S. leucophylla* numbered no more than three. Therefore, the absolute nucleotide differences among representatives of *S. leucophylla* (a species with a continuous range) were comparable with *S. alata* and *S. rubra* (two species with disjunct ranges). No branches supporting infraspecific relationships were recovered in the strict consensus tree for any of these three species. One interpretation of this finding is that present disjunct populations have been founded only recently (cf. Godt and Hamrick 1998).

Discussion

The place of origin for the ancestral Sarraceniaceae is equivocal. However, with *Darlingtonia's* position in the cladograms (Figs. 1, 2), it appears that a subtropical North American origin is at least as likely as a Neotropical one for the family. As suggested by Bayer et al. (1996), if Sarraceniaceae originated in subtropical North America, then *Heliamphora* may have originated by a single long-distant dispersal event. However, if Sarraceniaceae had a Neotropical origin, then two dispersal events may have occurred to account for the present distribution (Bayer et al. 1996). Because other previously mentioned scenarios are also possible (cf. Croizat 1960; McDaniel 1966; Mellichamp 1983; Renner 1989), the origin and migration of ancestral Sarraceniaceae remain unresolved.

Although all relationships have not been resolved, the present analysis brings new insight into the evolution of *Sarracenia*. One of the major findings of this study, is that *S. purpurea* is sister to all remaining species in *Sarracenia* and that a major subsequent dichotomy in the evolution of the genus has resulted in one clade composed of *S. minor, S. psittacina*, and *S. flava* and second clade composed of *S. alata, S. rubra, S. oreophila*, and *S. leucophylla*.

Another major finding of this research is that the named subspecies of *Sarracenia rubra* do not appear in a discernable phylogenetic structure (Figs. 1, 2). The hypothesis by Romeo et al. (1977) that the *S. rubra* complex is derived within the genus was supported by the complex's position in the cladograms (Figs. 1, 2). Although the representatives of *S. alata* were moderately supported as a monophyletic group, the systematic relationships among the five subspecies of *S. rubra* were unresolved. Similarly, Bayer et al.'s (1996) analysis failed to resolve the relationship between *S. rubra* and *S. jonesii*.

Therefore, although each subspecies may be disjunct and exhibit minor morphological differences, the naming of *S. rubra* subspecies may be tenuous. These findings support McDaniel's (1971) contention that the naming of infraspecific taxa of *S. rubra* is not warranted. Additionally, the naming of *S. jonesii* and *S. alabamensis* as separate species is not supported by this study. Although there is little molecular distinction between *S. oreophila* and the representatives of *S. rubra*, the two taxa are morphologically distinct and may be considered separate species, at least by the criteria embodied in the morphospecies concept.

In contrast, representatives from the named infraspecific taxa of *S. purpurea* appear in a resolved clade (Figs. 1, 2). If *S. purpurea* ssp. *purpurea* var. *burkii* is treated as a distinct species (i.e., *S. rosea*), then the number of species in the genus stands at nine. By this logic, each of the remaining three infraspecific taxa could also be named as distinct species which would increase the number of species in the genus to twelve.

An additional finding of this research concerns the putative affinity among *Sarracenia psittacina, S. flava* and *S. minor*. As noted previously, this same clade was recovered in Bayer et al.'s (1996) analysis. However, other studies have suggested different affinities for these three taxa. For example, *S. psittacina* has been aligned with *S. purpurea* (McDaniel 1966; Schnell and Krider 1976). Suggested affinities for *S. flava* include *S. leucophylla* (McDaniel 1966), *S. oreophila* (Schnell and Krider 1976; Schnell 1978) and *S. alata* (McDaniel 1966; Schnell 1978). MacFarlane (1893) considered *S. minor* to be similar to

the ancestral form of *Sarracenia* and, therefore, it would occupy the basal position in the genus. McDaniel (1966) suggested that *S. minor* has a close affinity with *S. rubra*. In the phenetic study by Schnell and Krider (1976), *S. minor* appeared isolated and clustered with no other taxa.

Future research aiming to clarify these remaining unresolved relationships within *Sarracenia* must employ DNA sequences with very high mutation rates. Although the ITS regions and the first kb of the 26S gene exhibit comparatively high mutation rates, it is apparent that more informative characters will be necessary to bring a higher degree of resolution to the genus. However, it is unclear what other sequence fragments may be useful in this regard. Future research efforts may resolve, for example, the relationships among the morphologically distinct *S. alata, S. rubra*, and *S. oreophila*. The resolution of systematic relationships among the morphologically similar subspecies of *S. rubra* may prove more problematic.

The recovery of a completely resolved and robustly supported phylogeny of *Sarracenia* remains elusive. Perhaps the problem was described best by Schnell and Krider (1976) who stated that the genus is probably incompletely differentiated with all species very closely related in a genetic and evolutionary sense. In a genus that easily produces natural hybrids (cf. DeBuhr 1975; Schnell and Krider 1976), there is a distinct possibility that several recognized species of *Sarracenia* have arisen through hybridization and introgression (cf. Anderson 1953; Stebbins 1959; Riesenberg and Eilstrand 1993; Arnold and Hedges 1995; McDade 1995; Bayer et al. 1996; Ellison 2004). Such processes result in reticulate evolutionary patterns that are difficult to decipher.

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GEOGRAPHY AND MORPHOLOGY OF THE *BROMUS CARINATUS* (POACEAE: BROMEAE) COMPLEX

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Abstract

The *Bromus carinatus* complex comprises several cleistogamous taxa that have been recognized at a variety of taxonomic levels. Our study focused on three taxa: *B. carinatus s.s.*, *B. marginatus*, and *B. polyanthus*, that have received varied taxonomic treatment. We mapped the collection sites of 673 specimens belonging to these taxa to determine whether their geographic distribution would support their recognition as species. We examined the characters customarily used to distinguish among the three entities: longevity, blade width, awn length, sheath vestiture, and lemma vestiture. The geographic data do not support the value of blade width as a taxonomic character but provide some support for use of awn length and the two vestiture characters. Of the three taxa, *B. polyanthus*, characterized as having glabrous sheaths and lemmas and, usually, short awns, was the most geographically distinct taxon. *Bromus carinatus sensu stricto* and *B. marginatus* showed some separation, the former being primarily a coastal taxon and the latter primarily an inland taxon. Based on our observations and published molecular data, we propose that *B. carinatus* and *B. marginatus* be treated as *B. carinatus* var. *carinatus* and **B. carinatus** var. **marginatus** (Nees *ex* Steud.) Barkworth & Anderton, *comb. nov.* respectively, and that *B. polyanthus* be treated as a species.

Key Words: *Bromus*, geography, distribution, morphology, taxonomy, nomenclature, *Poaceae*.

Bromus L. includes approximately 150 species, distributed among 6 sections (Clayton and Renvoize 1986) that are sometimes recognized as genera (e.g., Tsvelev 1976). Section *Ceratochloa* (P. Beauv.) Griseb. is native to the western hemisphere. Its members differ from those of other sections in having strongly keeled lemmas and 3–5-veined lower glumes.

The number of species recognized in sect. *Ceratochloa* varies considerably (Table 1). Hitchcock (1935) recognized five species in his treatment of grasses for the contiguous United States: *B. catharticus* Vahl, *B. sitchensis* Trin., *B. aleutensis* Trin. *ex* Griseb., *B. breviaristatus* Buckley, and *B. carinatus* (Hook. & Arn.). He acknowledged, however, the existence of many forms (using the word in its general, not nomenclatural, sense) of *B. carinatus* that ". . . are connected by numerous intergrades [and] can be distinguished only arbitrarily" (p. 38). He listed *B. marginatus* Nees *ex* Steud., *B. maritimus* (Piper) Hitchc., and *B. polyanthus* Scribn. *ex* Shear as names that applied to such forms.

Some subsequent taxonomists have recognized more species than Hitchcock (e.g., Kearney and Peebles 1942; Chase (*in* Hitchcock 1951); Davis 1952; Harrington 1954; Munz and Keck 1959); others have recognized fewer (e.g., Hitchcock 1969; Scoggan 1978; Wilkens and Painter 1993). There have been similar disagreements concerning the treatment of Mexican and Central and South American members of sect. *Ceratochloa* (e.g., Soderstrom and Beaman 1968; Planchuelo and Peterson 2000; Massa et al. 2004).

Those adopting a broad interpretation of *B. carinatus* have generally cited papers by Stebbins and Tobgy (1944) and Harlan (1945) in support of their treatment. Stebbins and Tobgy (1944) suggested that *B. carinatus* is probably an intersectional polyploid, combining three sets of chromosomes from sect. *Ceratochloa* and one from sect. *Bromopsis* Dumort. [=sect. *Pnigma* Dumort]. They also suggested that the low elevation, coastal members of the complex (*B. carinatus s.s.*, *B. sitchensis* Trin., and *B. aleutensis* Trin. *ex* Griseb.) might involve a different *Pnigma* parent from the inland species (*B. marginatus*, *B. polyanthus*, and *B. breviaristatus* Buckley), pointing out that diploid members of

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TABLE 1. COMPARISON OF THE TREATMENT OF *BROMUS* SECT. *CERATOCHLOA* IN DIFFERENT WORKS. Cells with the same shading density were recognized as a single species. Y—name used at species level. Unshaded empty cells: taxon not mentioned, usually because it is absent from the region treated, occasionally because only limited synonymy was provided. Sources: ASH 1—Hitchcock (1935); ASH 2—Hitchcock (1951); CLH—C.L. Hitchcock (1969); HDH—Harrington (1954); HJS—Scoggan (1978); K&P—Kearney and Peebles (1942); LP—Pavlick (1995); M&K—Munz and Keck (1959); RJD—Davis (1952); W&P—Wilken and Painter (1993); W&W—Weber and Wittmann (1992). [1] *Bromus luzonensis* used to be called *B. subvelutinus* Shear; *B. luzonensis* is the earlier name (Veldkamp 1990). [2] *Bromus willdenowii* used to be called, incorrectly, *B. unioloides* Kunth.

	ASH1	K&P	ASH2	RJD	HDH	M&K	CLH	HJS	W&W	W&P	LP
	1935	1942	1951	1952	1954	1959	1969	1978	1992	1993	1995
	48	AZ NM	48	ID	CO	CA	Pac. NW	Can.	CO	CA	FNA
B. carinatus	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y
B. marginatus		Y	Y	Y	Y	Y					Y
B. polyanthus		Y	Y	Y	Y	Y					Y
B. arizonicus			Y			Y				Y	Y
B. maritimus			Y			Y					Y
B. breviaristatus	Y		Y	Y		Y					
B. luzonensis[1]											Y
B. catharticus	Y	Y	Y		Y	Y		Y		Y	Y
B. haenkeanus						Y					
B. willdenowii[2]									Y		
B. sitchensis	Y		Y				Y	Y		Y	Y
B. aleutensis	Y		Y								Y
B. stamineus						Y				Y	Y

sect. *Pnigma* (e.g., *B. grandis* [Shear] Hitchc., *B. orcuttianus* Vasey, and *B. vulgaris* [Hook.] Shear) have narrow lemmas and long awns and are primarily coastal, whereas the diploid species with broad lemmas and short awns (e.g., *B. anomalus* Rupr. *ex* E. Fourn., *B. ciliatus* L., *B. frondosus* [Shear] Wooten & Standley, *B. kalmii* A.Gray, and *B. suksdorfii* Vasey) are inland or high elevation species.

Dremann (Email to Barkworth; November, 2004) stated that, in the San Francisco Bay region, there were at least five morphologically distinct ecotypes based on his common garden studies: dwarf, small-seeded individuals from windswept coastal populations; matlike sand dune populations; dwarf, hairy, fast-maturing serpentine populations; tall populations from high rainfall areas; and dwarf, hairy, large-seeded populations growing in full sun within areas of low rainfall. He added that there were gradations between these extremes with the region.

This study arose from problems encountered in editing Pavlick's (1995) revision of *Bromus* in North America north of Mexico, which he had also submitted as his treatment of *Bromus* for the *Flora of North America* (FNA) series. Unfortunately, Pavlick's health problems precluded his participation in the editing process. One major editorial problem for the FNA series was the need for more precise and better documented distribution data, the other was for increased parallelism in the descriptions.

Pavlick included "shaded area" maps in his revision, but the FNA grass volumes use maps generated from a database system that requires county level data for sites in the contiguous United States and locality data for sites in Canada, Alaska, and Greenland. For species whose taxo-

TABLE 2. CHARACTERISTICS USED TO DISTINGUISH AMONG *BROMUS CARINATUS S.S.*, *B. MARGINATUS*, AND *B. POLYANTHUS*. Those used by Pavlick (1995) are **boldfaced**. Sources: CLH—C.L. Hitchcock (1969); H&H—Holmgren and Holmgren (1977); HDH—Harrington (1954); K&P—Kearney and Peebles (1942); M&K—Munz and Keck (1959); RJD—Davis (1952); W&P—Wilken and Painter (1993).

	Bromus carinatus	*Bromus marginatus*	*Bromus polyanthus*
Longevity	**Annual or biennial** (RJD,HDH,M&K)	**Perennial** (M&K) Mostly perennial (HDH)	**Perennial** (RJD,HDH,M&K)
	Perennial, often flowering first season (CLH, W&P, H&H)		
Sheath vestiture	**Pilose to mostly glabrous, throat always with hairs** Pilose to nearly glabrous (HDH) Smooth or scabrous to sparsely pilose (M&K)	**Pilose to glabrous, throat always with hairs** Pubescent (K&P) Pilose (M&K)	**Mostly glabrous, sometimes hairy** Glabrous (K&P,M&K) Usually glabrous (HDH)
	Usually pilose, sometimes glabrous (CLH, H&H) Glabrous to soft-hairy (W&P)		
Blade width (mm)	**3–6** 3–10 (M&K)	**6–12** 4–12 (HDH) 4–8(12) (M&K)	**No information** 5–15 (M&K)
	(2)3–12(15) (CLH) (2)3.5–9(12) (H&H) 3–15(W&P)		
Glume vestiture		**Scabrous or pubescent** Pubescent (HDH) Scabrous or scabrous-pubescent (M&K)	**Smooth or scabrous** Glabrous or scabrous (HDH)
	Glabrous to soft-hairy (WP)		
Lemma vestiture	**Usually pubescent, sometimes scabrous** Appressed pubescent, rarely glabrous (HDH)	**Pubescent or glabrous** Pubescent (K&P, RJD, HDH)	**Glabrous or scabrous** (K&P, RJD) Pubescent to puberulent (HDH)
	Glabrous, scabrous, or pubescent (CLH) Glabrous to scabrous to hirsute (H&H) Glabrous to densely short-hairy (W&P)		
Awn length (mm)	**6–8(15)** 7–15 (RJD,M&K,HDH)	**4–7** (M&K) < 7 (RJD) 4–6 (HDH)	**4–8** 4–6 (RJD,HDH,M&K)
	3–15 (CLH) (3)4–6(8) (H&H)		

nomic treatment has not changed, data are obtained from many sources (e.g., herbarium databases, floras, checklists, etc.); if taxonomic boundaries have been changed, as was the case for some of Pavlick's taxa, this approach cannot be used.

Pavlick (1995, p. 6) explained that his philosophical approach was ". . . mainly morphological-geographical, modified by available biosystematic evidence . . . . In all cases, the question was asked whether a species concept for a particular taxon would be useful to those that might use this treatment for ecological, resource management or other purposes." He noted that ". . . a number of sometimes neglected taxa are resurrected, and some taxa at infraspecific rank or no rank at all (...) are again treated as species." (*ibid.* p. 7).

Pavlick's treatment of members of the historically challenging *B. carinatus* complex was particularly controversial; some individuals expressed their dismay to Barkworth at his decision to resurrect species that recent works had included in *B. carinatus s.l.*; others praised his insight. In explaining his decision to adopt a narrow interpretation of *B. carinatus*, Pavlick stated that "Despite some intermediate forms, most populations of [sect.] *Ceratochloa* are often easily recognized to species on the basis of their morphology and often occupy different ecological niches and/or geographic zones. There are a number of morphological characters which separate each of the taxa" (*ibid.* p. 95).

His descriptions failed to substantiate the last statement; identification of *B. carinatus*, *B. marginatus*, and *B. polyanthus* was essentially dependent on one or two characters. Moreover, initial examination of specimens suggested that variation in the most frequently used characters was continuous. Consequently, we decided to examine specimens from throughout the range of the three taxa in order to substantiate any decisions we made concerning their treatment in volume 24 of the *Flora of North America* (in prep.). Time constraints precluded extending the study to other taxa in sect. *Ceratochloa.*

In Pavlick's (1995) treatment, the only character distinguishing *B. carinatus* from *B. marginatus* and *B. polyanthus* was longevity (annual or biennial versus perennial) (Table 2). *Bromus carinatus* and *B. marginatus* are described as differing in blade width (3–6 mm versus 6–12 mm); no information on blade width is given for *B. polyanthus*. Other taxonomists have used lemma awn length and lemma and sheath throat pubescence, sometimes in combination with longevity to distinguish among the three taxa (Table 2).

We decided to examine the relationship between the morphological characteristics and geographic distribution of plants belonging to *B. carinatus s.s.*, *B. marginatus*, and *B. polyanthus* more closely, focusing on characters traditionally used for their identification, to determine whether the taxa recognized by Pavlick were morphologically and geographically distinct.

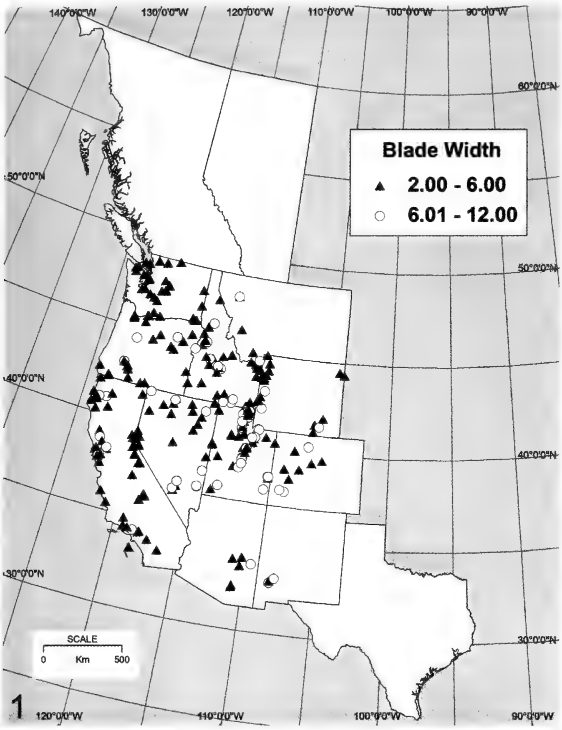
Soreng et al. (2003) recognized two varieties within *B. polyanthus*, var. *paniculatus* Shear and var. *polyanthus.* Pavlick (1995) equivocated with respect to their status, stating that they "are sometimes separated," var. *polyanthus* having erect, contracted panicles, short, erect or ascending branches, and awns 4–6 mm long, and var. *paniculatus* having nodding, open panicles, spreading branches, and awns up to 8 mm long. We measured the lowest panicle branch lengths on a sample of *B. polyanthus* specimens to see whether longer branches were associated with more open panicles and longer awns.

Methods

We examined 702 herbarium specimens from five herbaria: ARIZ (170 specimens), WTU (88 specimens), NMCR (57 specimens), UTC (269 specimens), and V (118 specimens) (Herbarium codes from Holmgren et al. 1977.) Of the 702 specimens, 29 could not be georeferenced because the label data were inadequate; 30 were not mapped because they were cultivated plants. Because our primary goal was evaluation of Pavlick's treatment, we focused on four of the characters he and earlier taxonomists used for taxonomic delimitation of *Bromus carinatus*, *B. marginatus*, and *B. polyanthus* (Table 2). We were alert to the possibility that there might be other characters that could be used for taxonomic delimitation within the complex, but were unable to identify any.

Longevity was not scored because it is often difficult to determine on herbarium specimens. Blade width was measured on what appeared to be the widest blade of a specimen; it was obtained only for specimens from WTU and UTC for reasons discussed in the following section. Awn lengths were obtained by averaging the length of the longest three awns on a specimen. Sheath throat and lemma pubescence were scored as follows: G for glabrous or scabrous, P– if only a few hairs were visible or if only some sheath throats or lemmas had hairs, P for visible pubescence on most lemmas or sheath throats, and P+ for exceptionally thick pubescence on most lemmas or sheath throats. Panicle branch length was measured on the longest branch at the lowest node on 70 specimens that, according to our criteria, belonged to *B. polyanthus*.

Few specimen labels included georeferencing data. We obtained latitude/longitude data for those lacking them by a variety of methods, depending on the label information. Specimens



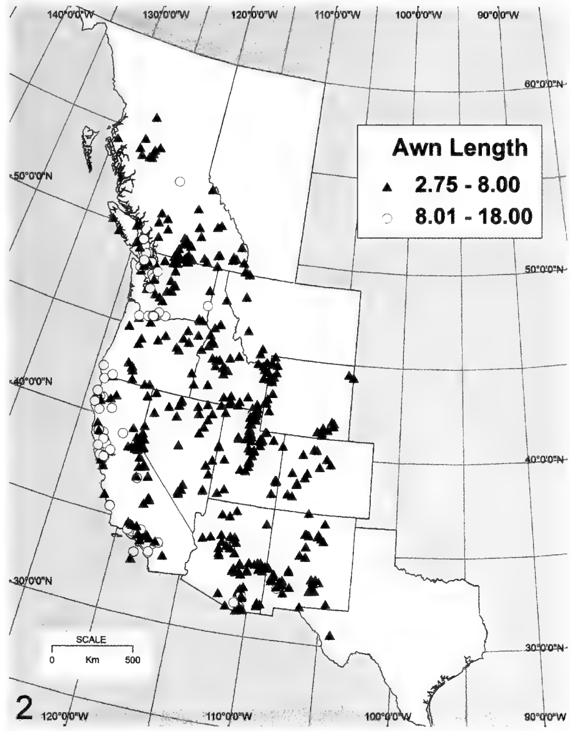


FIG. 1. Distribution of specimens with blade widths narrower or wider than 6 mm. Only the 357 specimens from WTU and UTC were included in this portion of the study.
FIG. 2. Distribution of specimens with awns shorter or longer than 8 mm. Locations of all 673 mapped specimens are shown.

with township, range, and section data were georeferenced using Wefald's (2003) TRS2LL program. For U.S. specimens lacking such data, we used the Geographic Names Information System, refining the estimate where feasible by using maps from TopoZone (Maps a la Carte, 2004). For Canadian specimens, we used Natural Resources Canada's Geographical Names of Canada website. Because we were unable to evaluate the accuracy of specimen label information, our georeference data are only estimates of the original collecting locality, but they are sufficiently accurate to portray the general geographic distribution of the specimens examined; they are not sufficiently accurate to determine ecological characteristics of the collecting site.

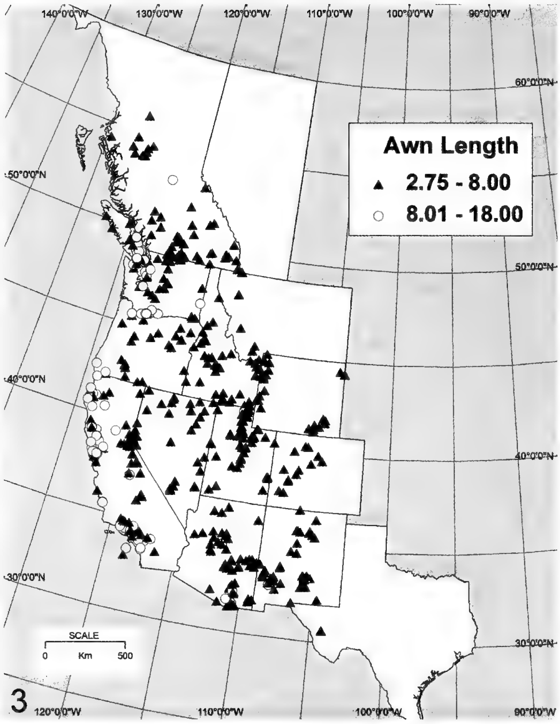
The georeferenced data were combined with the morphological data to relate the morphological variation to geographic distribution. For this analysis, we divided the two continuous characters, awn length and blade width, into two classes each, using breaks indicated by previous treatments (<7 mm and >7 mm, and 3–6 mm and 6–12 mm, respectively). In addition, we used Jenks optimization to calculate the best "natural break" in the data, based on the assumption that two classes were present. Jenks optimization partitions data into classes by minimizing the possible total error (the sum of absolute deviations based on the class median or the sum of squared deviations about the class mean) (Jenks 1967).

Maps were drawn using ArcMap 9.1 (ESRI 1999–2005) and Albers Equal Area Conic projection, datum NAD 83. The layouts were prepared using Creative Suite 2 (Adobe 2005).

RESULTS

The specimens examined came from a wide area (Figs. 1–4; Appendix I). Nevertheless, maps developed from a wider range of sources (Intermountain Herbarium 1999+) demonstrate that Yukon Territory, Alberta, Saskatchewan, Montana, North Dakota, Wyoming, Colorado, South Dakota, Kansas, northern Arizona, northern New Mexico, and Texas are not well represented in this study. The areas represented, however, include those in which the three taxa that were the focus of this study are most controversial (Table 1).

According to Pavlick, *Bromus carinatus s.s.* and *B. marginatus* differ in their blade widths; those of *B. carinatus* being up to 6 mm wide and those of *B. marginatus* being 6+ mm wide. He did not provide information about blade widths in *B. polyanthus.* Mapping of specimens from WTU



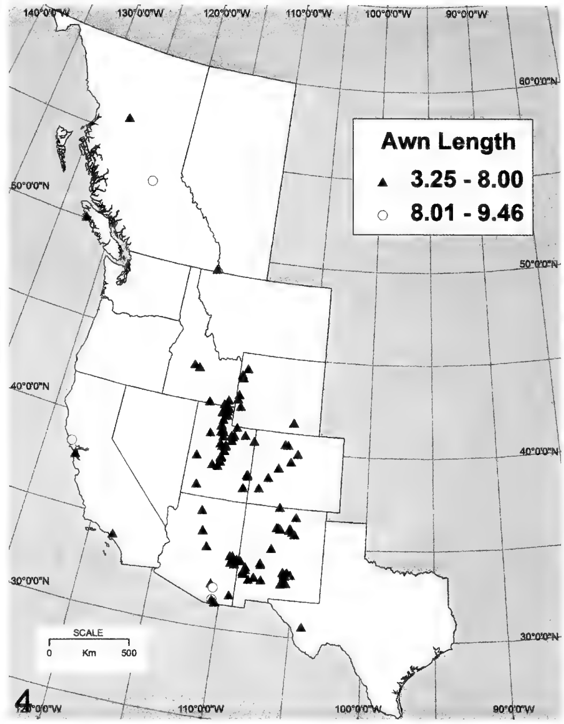


FIG. 3. Distribution of specimens with hairs on their throats and/or lemmas and awns longer or shorter than 8 mm (i.e., *Bromus carinatus* vars. *carinatus* and *marginatus*, respectively).
FIG. 4. Distribution of specimens with glabrous throats and lemmas (i.e., *Bromus polyanthus*) showing origin of specimens with awns shorter and longer than 8 mm.

and UTC revealed no geographic separation of plants with blade widths above and below 6 mm (Fig. 1). Jenk's optimization divided the specimens into two categories at 5 mm. These two categories also were not geographically segregated. We also mapped the specimens with glabrous lemmas and sheaths, (i.e., *B. polyanthus*). These too exhibited no geographic separation between wide- and narrow-leaved specimens (not shown). Thus, we concluded that blade width is not a useful taxonomic character within the taxa under consideration and excluded it from further examination.

Awn length has been used to distinguish *B. carinatus* from both *B. marginatus* and *B. polyanthus* (Table 2). Mapping revealed that almost all specimens with awns 8–18 mm long came from near the coast whereas most specimens with short awns came from inland locations (Fig. 2). Jenks optimization divided the specimens at 7.45 mm; the map using this value as the break point (not shown) was little different from that obtained using 8 mm.

The geographic separation of the short- and long-awned specimens was not absolute. Some short-awned specimens came from near the coast and some long-awned specimens from inland areas in central British Columbia, along the Snake River near the Washington-Idaho border, and southern Arizona and New Mexico. It is, of course, possible that the specimens concerned were collected because they differed from others in the region or that they were collected in unusual habitats within the region. We concluded that the geographic separation, although incomplete, tended to support the taxonomic value of awn length for the portion of the *B. carinatus* complex included in our study.

TABLE 3. NUMBER OF SPECIMENS BY THEIR COMBINATION OF PUBESCENCE CHARACTERISTICS.

Lemma throat	Glabrous	Sparsely pubescent	Moderately pubescent	Densely pubescent	Total
Glabrous	155	9	26	1	**191**
Sparsely pubescent	18	6	40	2	**66**
Moderately pubescent	43	27	313	6	**389**
Densely pubescent	0	3	16	8	**27**
Total	**216**	**45**	**395**	**17**	**673**

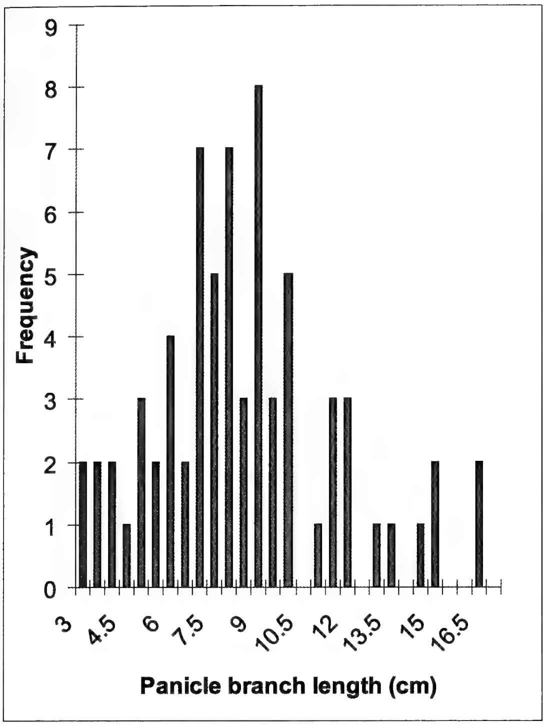


FIG. 5. Histogram of lowest panicle branch lengths in *Bromus polyanthus*.

Vestiture of the sheath and lemma have also been used to distinguish among *B. carinatus*, *B. marginatus*, and *B. polyanthus.* Existing descriptions suggest that there is variation in both characters, but particularly sheath vestiture, within each taxon. We found the association between throat and lemma vestiture was high (Table 3). Of the 673 specimens mapped, almost half (313) had moderately pubescent throats and lemmas; the second largest class of specimens had glabrous lemmas and throats (155). Glabrous lemmas were never found on plants with densely pubescent throats; one specimen with densely pubescent lemmas had glabrous throats. Specimens with hairs on the throats and/or lemmas came from throughout the range of specimens in this study (Fig. 3), whereas those with completely glabrous throats and lemmas, which would correspond to *B. polyanthus*, came primarily from the Rocky Mountains (Fig. 4). Eight of the completely glabrous specimens had awns longer than 8 mm; one was from British Columbia, two from coastal California, three from southern Arizona and two from New Mexico.

Panicle branch lengths for *B. polyanthus* were essentially unimodal (Fig. 5). Some of the specimens with branches longer than 11 cm had open panicles; it was impossible to determine whether the others might have had open panicles if collected slightly later in the season. The correlation between panicle branch length and awn length was 0.44.

DISCUSSION

Our study demonstrates that the taxa Pavlick (1995) identified as *Bromus carinatus*, *B. marginatus*, and *B. polyanthus* have somewhat different geographic distributions, which supports their recognition as distinct taxa at some level. The geographic separation between long-awned and short-awned specimens, as well as that between glabrous and pubescent specimens, supports the use of awn length and pubescence of sheath throats and lemmas as characters delimiting distinct taxa. There were not as many long-awned glabrous specimens (8) as would be expected (26.486) if awn length and pubescence were independent characters (chi-square statistic $= 20.2177, < 0.0001$).

None of the entities circumscribed by the characters examined in this study were completely geographically distinct. Moreover, the morphological separation of specimens based on pubescence of lemmas and sheath throats and average awn length glossed over the fact that several specimens had awns either just under or just over 8.0 mm; variation in pubescence density was also continuous.

The most morphologically distinct group included specimens with completely glabrous sheath throats and lemmas; most also had awns shorter than 8 mm. Specimens with this combination of characteristics came primarily from the Rocky Mountains (Fig. 4). They correspond to *B. polyanthus*.

Massa and Larson's (2005) phylogeographic study of *B. carinatus* confirmed that *B. polyanthus* is more distinct than either *B. carinatus* or *B. marginatus*. Using AFLP, they identified four genetically distinct groups among their samples, all of which they referred to *B. carinatus sensu lato*. Examination of the vouchers deposited at UTC revealed that all three accessions in their group 4 belong to *B. polyanthus*, both morphologically and geographically.

The other specimens in Massa and Larson's (2005) study had awns less than 8 mm long, which placed them within *B. marginatus*. They stated that two of them, CAR03 (PI 202202) and CAR04 (PI 202203), came from seed accessions derived from collections made in Marin County, in coastal California. Of these two, CAR03 was notable for having some awns longer than 8 mm. All the voucher specimens were made from plants grown in a uniform garden near Logan, Utah.

The PI numbers enabled us to obtain additional information for the accessions from the U.S.D.A.'s Germplasm Resource Information Network (U.S.D.A. 2005). Both accessions are

derived from seed collections made in 1955. Only PI 232202 was collected in Marin County; PI 232203 is derived from multiple collections made throughout the western U.S. The accessions have been maintained by growing seed up and harvesting seed from the mature plants. Initially, the accessions were grown out in Ames, Iowa; since 1985 they have been grown out in Pullman, Washington. While at Ames and for the first five years at Pullman, seed accessions were grown up without being isolated from other accessions of the same species. It is not known how many times new seed has been collected. This history would have favored a slow shift in gene frequencies to genotypes that are adapted to the climatic conditions at interior locations rather than those of coastal California. Moreover, as Harlan (1945) demonstrated, the taxa are only predominantly cleistogamous; outcrossing may also have occurred between descendants of the original accessions and those of other accessions.

Their history reduces the taxonomic value of the accessions in GRIN. It is possible that the population from which PI 232202 was originally obtained corresponded to *B. carinatus s.s.* There were, however, many wild-collected specimens that, like PI 232202, had some awns more than 8 mm long even though the majority were shorter. Neither the study by Massa and Larson (2005) nor this study eliminated the possibility that the short-awned specimens growing near the coast are environmentally modified representatives of a long-awned taxon. We are also unable to reject Stebbins and Tobgy's (1944) hypothesis that the shorter awned plants have a different parentage from the longer awned plants.

Pavlick (1995) argued that groups should be recognized as species if doing so would "be useful to those that might use this treatment for ecological, resource management or other purposes". We agree that some nomenclatural difference is desirable for taxa that appear to have different ecological characteristics; we do not agree that they need to be recognized as species. Based on the morphological, geographic, and genetic data available, we propose that *B. marginatus* and *B. carinatus* be treated as conspecific taxa and *B. polyanthus* as a distinct species. For consistency with Pavlick's treatment of other species, we are proposing that *B. carinatus sensu stricto* and *B. marginatus* be recognized as varieties. The following key summarizes our findings.

1. Lemmas and sheaths completely glabrous, sometimes scabrous. . . . . *B. polyanthus*
1. Lemmas and/or sheaths with some hairs . . . . *B. carinatus*
   2. Most awns 8–17 mm long . . . . *B. carinatus* var. *carinatus*
   2. Most awns 4–7 mm long . . . . *B. carinatus* var. *marginatus*

Bromus carinatus var. **marginatus** (Nees) Barkworth & Anderton, *comb. nov.* Basionym: *Bromus marginatus* Nees *in* Steud., Syn. pl. Glum. 1:322 (1854). Type: Fragment US865445!; Columbia River, Douglas.

Scoggan (1978) attributed this combination to A.S. Hitchcock, but there is no evidence that Hitchcock actually made the combination.

Our data leave the status of the varieties of *B. polyanthus* unclear. Using the criteria that we did for identifying the species, there were a few specimens of *B. polyanthus* that conformed to var. *paniculatus* but they appeared to be extremes of a continuous range of variation. If, however, awn length were given greater weight in identification, Arizonan and New Mexican specimens that we placed in *B. carinatus* var. *carinatus* because they had some hairs on their lemmas or sheaths would be identified as *B. polyanthus* var. *paniculatus.* An additional possibility is that they, together with the long branched specimens we identified as *B. polyanthus*, represent a new, unrecognized taxon.

Clearly, a better understanding of the bases of variability within *B. carinatus* and its relatives is essential to their more satisfactory taxonomic treatment. Developing such an understanding requires an interdisciplinary study involving experimental, cytogenetic, and molecular investigations of wild populations.

Volume 24 of the *Flora of North America* series, which is scheduled for publication in the fall of 2006, will contain keys, descriptions, and illustrations for the three taxa that were the focus of this study as well as the other taxa of *Bromus* that have been found in North America north of Mexico. We hope its publication will stimulate a new round of collaborative, interdisciplinary studies of the genus.

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Appendix I Representative Specimens Examined

Because we did not intend this paper as a revisionary study, we recorded only the data required to relocate an individual specimen among those on loan. Additional specimen information for UTC and WTU specimens is available from the Global Biodiversity Information Facility (2005+). For specimens from NMCR, we include the first collector's initials and collection number because they have no accession number. Canadian specimens do not list county; we show the latitude and longitude of representative specimens. As noted in the text, most such data were obtained retrospectively.

Bromus carinatus var. ***carinatus*** **CANADA. BRITISH COLUMBIA**. V 102110 (48.55N 123.417W), V 113786 (48.833N 123.383W), V 129566 (48.933N 123.45W), V 132360 (49.192N 123.925W), V 132364 (50.9N 119.55W), V132661 (49.183N, 123.933W) V 139379 (48.85N 123.467W), V 151534 (48.417N 123.267W), V

17035 (53N 122.5W), V 177897 (48.658N 123.742W), V 177898 (48.417N 123.667W), V 178359 (49.5N 124.2W), V 178365 (49.5N 124.217W), V 179229 (48.517N 123.417), V 185898 (48.808N 123.63W), V 187492 (48.433N 123.633W), V 20334 (52.85N 132.183W), V 23625 (48.65N 123.4W), V 24304 (50.1N 127.5W), V 453 (48.45N 123.3W), V 467 (54.217N 128.367W), V 469 (48.26N 123.367W), V 66153 (48.5N 123.358), V 66179 (48.27N 123.283W), V 66294 (48.55N 123.458W), V 66352 (48.4N 123.367W), V 66353 (48.625N 123.442W), V 66369 (48.667N 123.400W), V 66386 (48.692N 123.475W), V 66402 (48.683N 123.467W), V 66426 (48.45N 123.467W), V 66555 (48.6N 123.467W), V 75438 (53.05N 119.233W), V 82164 (48.833N 123.517W), V 87217 (48.8N 123.2W), V 8889 (48.55N 123.567W), V 95298 (48.783N 123.15W), V 95586 (49.2N 123.933W), V 96687 (48.43N 123.35W), V 97297 (48.85N 123.283W), V 97389 (48.933N 123.45W), V 98252 (48.483N 123.533W), V 98269 (48.808N 123.908W), V 98535 (48.8N 123.267W). **UNITED STATES. ARIZONA**. Apache. UTC 80085; Cochise ARIZ 255026; Gila ARIZ 329059; Mohave UTC 104006; Pima UTC 238268; Santa Cruz ARIZ 91978; **CALIFORNIA.** Alameda ARIZ 09175; Alpine UTC 195685; Contra Costa UTC 57852; Del Norte WTU 205599; El Dorado ARIZ 30307; Humboldt UTC 99436; Lake UTC 85585; Los Angeles WTU 65528; Madera ARIZ 373904, UTC 116447, WTU 224452; Marin ARIZ 130024, UTC 107945, UTC 107958, UTC 59699, UTC 94689; Mariposa ARIZ 373897; Mendocino ARIZ 373886, ARIZ 373887, ARIZ 373893, ARIZ 373893, ARIZ 373894, ARIZ 373894; Mono UTC 111611; Monterey ARIZ 333966; Napa UTC 230836, UTC 99439; Riverside, ARIZ 317886, ARIZ 317886, UTC 174024, UTC 227709, UTC 236784; San Bernardino ARIZ 258400, ARIZ 373888, ARIZ 373888; San Diego ARIZ 308099, ARIZ 308099, UTC 210342; San Francisco UTC 116608, UTC 126465; San Luis Obispo ARIZ 105998, WTU 121664; San Mateo ARIZ 261182; Santa Barbara UTC 237960; Santa Clara WTU 46684; Shasta WTU 132637; Solano UTC 230923; Sonoma ARIZ 175403, UTC 242988; Trinity WTU 287090; Tulare WTU 192108; Ventura UTC 209582, WTU 116574, WTU 132645; Yolo UTC 147488, UTC 208828; Yuba ARIZ 141375. **NEW MEXICO.** Catron NMCR KA 7578; Eddy NMCR KA 2256; Grant UTC 92709; Lincoln ARIZ 348355; Otero NMCR KA 3100; Sandoval NMCR KA 2547; Sierra ARIZ 126241; Socorro NMCR KA 8433; Torrance NMCR KA 6289; Valencia NMCR KP 391. **OREGON.** Curry WTU 259120; Hood River NMCR JB 6291937; Jackson UTC 243802; Josephine WTU 345697; Lake WTU 25849; Multnomah WTU 238041; Polk ARIZ 258854. **TEXAS.** Jeff Davis ARIZ 373907. **UTAH.** Cache UTC 105779, UTC 93592. **WASHINGTON.** Clallam WTU 313876, WTU 32987; Jefferson WTU 288995; King WTU 54547; Kitsap WTU 288997; Klickitat, UTC 233912, V 44679, WTU 233153, WTU 233970, WTU 233971, WTU 237814, WTU 272747, WTU 272748, WTU 335048, WTU 351971; Pierce WTU 54558; San Juan V 123290; Skagit WTU 233902, WTU 269172; Snohomish ARIZ 373905, ARIZ 373905; Thurston WTU 345274; Whitman WTU 66518.

Bromus carinatus var. ***marginatus***. **CANADA. BRITISH COLUMBIA.** V 11102B (55.95N 126.617W), V 111787 (49.067N 120.183W), V 11304 (49.85N 123W), V 118639 (51.292N 123.542W), V 122663 (49.583N 126.617W), V 123150 (51.267N 116.6W), V 123175 (51.433N 116.417W), V 127864 (50.317N 122.717W), V 132417 (48.408N 123.625W), V 132723 (50.1N 125.2W), V 13300 (49.667N 117.283W), V 139961 (50.117N 120.45W), V 139968 (50.033N 120.425W), V 141175 (49.133N 114.583W), V 141201 (49.783N 115.867W), V 141845 (49.9N 120.617W), V 142109 (49.825N 119.867W), V 147784 (49.583N 114.85W), V 147785 (50.367N 115.333W), V 147790 (54.117N 127.208W), V 148719 (49.836N 120.607W), V 148747 (49.054N 118.849W), V 158408 (49.067N 121.133W), V 16395 (49.6N 115.883W), V 166870 (50.608N 123.33W), V167607 (49.717N 124.467W), V 168062 (48.533N 123.783W), V 168175 (49.333N 124.7W), V 171056 (49.583N 124.35W), V 175073 (49.7N 115.6W), V 176644 (54.45N 125.3W), V 17711 (54.233N 125.75W), V 17758 (53.8N 126.05W), V 177910 (49.542N 120.9W), V 178365 (49.5N 124.217W), V 179208 (49.717N 117.15W), V 179210 (49.35N 119.9W), V 179211 (49.183N 119.55W), V 179237 (48.817N 123.583W), V 179800 (49.107N 119.675W), V 18083 (49.117N 120.867W), V 18112 (49.117N 120.65W), V 183614 (53.812N 125.925W), V 184038 (53.81N 125.787W), V 185257 (54.033N 125.775W), V 185288 (53.788N 126.833W), V 185433 (49.103N 119.673W), V 186873 (54.692N 126.998W), V 188539 (49.04N 124.338W), V 24476 (50.9N 122.617W), V 29530 (49.5N 117.283W), V 30853 (50.45N 119.2W), V 38852 (49.25N 124.8W), V 45566 (51.85N 120.067W), V 467 (54.217N 129.633W), V 483 (50.167N 120.667W), V 50594 (49.2N 119.833W), V 563 (51.283N 117.583W), V 56595 (51.15N 117.917W), V 66172 (48.45N 123.267W), V 66918 (49.067N 120.7W), V 67268 (49N 120.8W), V 67654 (49.033N 120.933W), V 67661 (49.783N 117.167W), V 68810 (49.267N 120.2W), V 68842 (49.05N 120.967W), V 87217 (48.783N 123.15W), V 88449 (49.133N 119.667W), V 88465 (49.183N 120.083W), V 90176 (49.117N 119.617W), V 90182 (49.117N 119.883W), V 91361 (49.017N 114.104W), V91396 (49.019N 114.106W), V 93615 (49.111N 114.147W), V 93942 (49.032N 114.158W), V 94621 (50.383N 122.35W), V 98620 (48.781N 123.267W), V 66918 (49.117N 120.883W). **UNITED STATES. ARIZONA.** Apache ARIZ 185846; Cochise ARIZ 252313, ARIZ 255027, ARIZ 304977, ARIZ 362097, ARIZ 53657; Coconino ARIZ 109921, ARIZ 109934, ARIZ 160175, ARIZ 196643, UTC 137339; Gila ARIZ 110684, ARIZ 130668, ARIZ 167685, ARIZ 291305, ARIZ 328570, ARIZ 39833, ARIZ 75100, ARIZ 75101, UTC 23485, UTC 23492; Maricopa, ARIZ 109920, ARIZ 37606; Mohave, ARIZ 329394, ARIZ 65255; Pima, ARIZ 133623a, ARIZ 17210, ARIZ 244490, ARIZ 249063; Pinal ARIZ 106150 ARIZ 109914, ARIZ 304300, ARIZ 312982; Yavapai ARIZ 10759, ARIZ 10760, ARIZ 14724, ARIZ 229031, ARIZ 241804, ARIZ 373890, ARIZ 37835, ARIZ 65257, ARIZ 91974. **CALIFORNIA.** Alpine UTC 17509, UTC 17522, UTC 195655, UTC 195680, UTC 195686; Contra Costa NMCR KP CA; El Dorado ARIZ 256250. ARIZ 256250; Humboldt UTC 99433, UTC 99437, WTU 206345, WTU 206981, WTU 219492; Inyo ARIZ 32578, ARIZ 32578 Los Angeles ARIZ 294645, ARIZ 302102, ARIZ 317429, ARIZ 317429, ARIZ 352150, ARIZ 69600; Madera ARIZ 373904; Marin ARIZ 130141, ARIZ 261182, UTC 107959, WTU 51135; Mariposa ARIZ 373897; Mendocino ARIZ 373889, ARIZ 373896, ARIZ 373896; Modoc UTC 101618, UTC 56895; Mono UTC 100739, UTC 103357, WTU 231660, WTU 52787; Monterey ARIZ 373885,

UTC 209583; Nevada ARIZ 20728, UTC 107972; Placer UTC 107960, UTC 108713; Plumas ARIZ 112556, ARIZ 112556, UTC 108716; San Bernardino ARIZ 15187, ARIZ 15187, ARIZ 309742, ARIZ 309742, ARIZ 353168; San Diego WTU 57961; Santa Barbara ARIZ 69643; Sierra ARIZ 20728; Trinity UTC 34823; Tulare WTU 179577; WTU 94997; Tuolumne WTU 60470; Ventura ARIZ 69600, ARIZ 69643. **COLORADO.** Gunnison ARIZ 353126, ARIZ 353127; Montrose ARIZ 353128, ARIZ 373908, ARIZ 373908; Routt UTC 245447. **IDAHO.** Adams UTC 108309, UTC 237666; Bear Lake WTU 300978; Blaine UTC 49452; Boise ARIZ 39178, UTC 220838, UTC 71135, UTC 71694; Camas WTU 299870; Cassia ARIZ 202880, UTC 139388, UTC 212111, UTC 234927, UTC 45233; Clark UTC 30055, UTC 46616; Custer UTC 49721; Fremont UTC 163480, UTC 42856, UTC 781; Idaho ARIZ 167569, ARIZ 167569, UTC 108299, UTC 108304, UTC 113111; Lemhi WTU 92426; Oneida UTC 122014; Power V 96380; Shoshone WTU 54560; Twin Falls UTC 150278; Valley UTC 134596, UTC 136838; Washington UTC 134238. **MONTANA.** Granite UTC 212558; Lake UTC 198297, UTC 198299; Madison UTC 72562. **NEVADA.** Carson City ARIZ 20729; Douglas ARIZ 20729, UTC 227143; Elko ARIZ 203021, ARIZ 22296, ARIZ 22296, UTC 108321, UTC 139389, UTC 191913, UTC 29593, WTU 268323; Humboldt ARIZ 203028, ARIZ 20716, ARIZ 20716, UTC 108257, UTC 139600, UTC 142599, WTU 268322; Lander UTC 153102; Lincoln UTC 141291, UTC 149274; Nye UTC 122098, UTC 128132, UTC 128156, UTC 128157, UTC 128158, UTC 128159, UTC 128160, UTC 128187; Washoe ARIZ 20717, ARIZ 373899, UTC 192488; White Pine ARIZ 203029, UTC 135470. **NEW MEXICO.** Bernalillo NMCR KA 7503; Catron NMCR KA 7578; Dona Ana NMCR JS 19; Eddy NMCR KA 2256; Grant NMCR JC 1284, NMCR KA 8380; Lincoln NMCR R 15, NMCR RW 30779; Otero NMCR KA 3100, UTC 151037; Sierra NMCR ER 1203, NMCR ER 636; Torrance NMCR KA 6289; Union NMCR R 15. **OREGON.** Baker UTC 202027, WTU 313742; Douglas UTC 34545, WTU 55398; Grant UTC 231408, WTU 154053, WTU 258386; Hood River WTU 25575; Jefferson WTU 224479; Josephine WTU 298349; Klamath UTC 108719, UTC 72657, WTU 298150, WTU 300994; Lake WTU 282410; Lane ARIZ 373891, ARIZ 373891; Linn UTC 80415; Malheur UTC 154348; Multnomah WTU 238040; Polk ARIZ 258854; Umatilla NMCR JB 28Jun1937; Wallowa WTU 262870; Wheeler WTU 144321. **TEXAS.** Jeff Davis ARIZ 373909; ARIZ 72958. **UTAH.** Cache ARIZ 107237, ARIZ 250271, UTC 217487, UTC 236800, UTC 236820, UTC 236841, UTC 236909, UTC 236979, UTC 237008, UTC 237980, UTC 238116, UTC 238127, UTC 79761; Davis UTC 22350; Garfield UTC 88997; Juab ARIZ 35690; Rich UTC 210376, UTC 237981; Salt Lake UTC 211202; Utah UTC 218590; Washington ARIZ 8803, ARIZ 8804. **WASHINGTON.** Asotin UTC 81926; Chelan V 137652, V 137654, WTU 124466, WTU 215242, WTU 288901, WTU 30296, WTU 322032, WTU 322035; Clallam WTU 21978; Columbia WTU 349068; Ferry UTC 61739; Garfield WTU 341137; Jefferson WTU 38322, WTU 39053; King WTU 23904, WTU 288808; Kittitas WTU 209672, WTU 218776, WTU 322034, WTU 357720; Klickitat WTU 228247, WTU 269216; Lewis WTU 324047; Okanogan V 137653, V 137655, V 137656, WTU 25511, WTU 332998; Pierce WTU 214880, WTU 329976; Skagit WTU 288885; Spokane WTU 14057; Whatcom WTU 25517, WTU 316970, WTU 86726; Whitman UTC 105616; Yakima WTU 31053. **WYOMING.** Albany, ARIZ 373900, ARIZ 45770, ARIZ 69634, UTC 157617, UTC 56755; Big Horn UTC 24473; Carbon ARIZ 125792, ARIZ 45620, UTC 153797; Lincoln UTC 155531, UTC 206601; Park UTC 172297, UTC 210095; Teton ARIZ 373901, UTC 106191, UTC 147161, UTC 185186, UTC 192955, UTC 207599, UTC 231568, UTC 28236.

Bromus polyanthus. **CANADA. BRITISH COLUMBIA.** V 011102A (55.95N 126.617W), V 141173 (49.133N 114.583W). **UNITED STATES. ARIZONA.** Apache ARIZ 109916, ARIZ 109932, ARIZ 109933, ARIZ 166683, ARIZ 176049, ARIZ 75102; Cochise ARIZ 10393; Coconino ARIZ 113981, ARIZ 113983, ARIZ 113985, ARIZ 257193, UTC 59763; Gila ARIZ 14898, ARIZ 65249; Pima ARIZ 247583, ARIZ 353122; Pinal ARIZ 113986; Santa Cruz ARIZ 223872, ARIZ 255220. **CALIFORNIA.** Los Angeles ARIZ 337375; San Francisco UTC 81091; Sonoma ARIZ 175403. **COLORADO.** Boulder ARIZ 353130; Jackson NMCR JB 23Jun1937; Montrose UTC 184729; Pitkin UTC 163490; Routt UTC 115602, UTC 115621; San Miguel UTC 179420; Summit UTC 163503. **IDAHO.** Blaine UTC 49451, UTC 71399; Cassia UTC 139599; Franklin UTC 213218, UTC 225805; Oneida UTC 782. **NEW MEXICO.** Catron ARIZ 185893, ARIZ 237501; NMCR KA 2333, NMCR KA 2348, NMCR KA 2364; Colfax NMCR JB 1941; Grant ARIZ 353129, NMCR KA 4652, UTC 113375, UTC 124119, UTC 139515; Lincoln ARIZ 109924, ARIZ 109927, ARIZ 109928, ARIZ 173185, ARIZ 173186, NMCR KA 2553, NMCR KA 2557, NMCR KA 2561, NMCR RW 31590, NMCR SA 13; Mora NMCR KA 6935; Otero NMCR KA 5166, NMCR JB 1512, NMCR KA 3098, NMCR KA 8342; Rio Arriba NMCR KA 4991; San Miguel ARIZ 173184, NMCR KA 2454, NMCR RH 76899; Sandoval NMCR JC 264, NMCR KA 2546, NMCR RH 72834; Santa Fe NMCR KA 2454; Sierra UTC 141541; Socorro NMCR KA 8433, NMCR KA 8469; Valencia NMCR KP 24Aug1933. **TEXAS.** Jeff Davis ARIZ 373907. **UTAH** Cache UTC 189028, UTC 20478, UTC 236893, UTC 29726, UTC 30101, UTC 30422, UTC 97270; Davis ARIZ 141064, UTC 23348; Duchesne UTC 146882; Grand UTC 181354, UTC 30102, V 142371; Iron UTC 2751; Salt Lake ARIZ 109929, ARIZ 117069, ARIZ 126498, ARIZ 127529; Sanpete ARIZ 109922, ARIZ 192268, UTC 108056; Sevier UTC 181752; Summit UTC 106940; Tooele UTC 156420; Uintah UTC 146883; Utah ARIZ 35268, ARIZ 35331, UTC 150717, UTC 150718, UTC 150724; Wasatch UTC 239393, UTC 239394. **WYOMING.** Carbon UTC 152076; Lincoln, UTC 154751, UTC 18039, UTC 192732, UTC 20479; Sublette UTC 228446; Teton NMCR GV 1949, UTC 131418, UTC 788.

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GENOTYPE DIVERSITY OF *SALSOLA TRAGUS* AND POTENTIAL ORIGINS OF A PREVIOUSLY UNIDENTIFIED INVASIVE *SALSOLA* FROM CALIFORNIA AND ARIZONA

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ABSTRACT

Various *Salsola* spp. have been introduced to the USA, and some of these are considered noxious or invasive in certain regions. The genus is taxonomically challenging, and recent morphological, cytological, and molecular work has shown that an unknown taxon, previously identified as *S. tragus*, but recently temporarily designated as Type B, with unknown origins, exists in California and Arizona. Type B's origins and identity are a point of concern for biological control efforts, as it is much less affected by fungal biological control agents than the sympatric invasive *S. tragus*. Initial studies in 2005 indicated that Type B is morphologically very similar to *S. kali* subsp. *austroafricana* which has been collected in southern Africa. Here we use DNA sequence data from a PEPC intron to compare USA and Old World specimens, and results indicate that *S. kali* subsp. *austroafricana* is genetically identical to Type B and distinct from *S. tragus*. It is unclear if *S. kali* subsp. *austroafricana* is native to southern Africa or to the northern hemisphere of the Old World, and further investigations in both regions are needed.

Key Words: PEPC, internal transcribed spacer, invasion, molecular systematics, Russian thistle, tumbleweed.

The native range of *Salsola tragus* L. (Russian thistle, family Chenopodiaceae) extends from northeastern China to the Atlantic coast of Europe and includes northern Africa (Rilke 1999). In North America, *S. tragus* was introduced into South Dakota in the 1870's, has spread throughout much of the USA and Canada, and is considered a noxious weed in California and Colorado.

Other *Salsola* species have been introduced to North America at various times (Mosyakin 1996; Mosyakin 2003; USDA 2005), including: *S. kali* L., *S. collina* Pall., and *S. paulsenii* Litv. of section *Kali* Dumort.; *S. soda* L. of section *Salsola* s.s.; and the more distantly related *S. vermiculata* L. of section *Caroxylon* (Thunb.) Fenzl.

Species level nomenclature within *Salsola* sect. *Salsola* s.l. has undergone many revisions and numerous alternate applications. Rilke (1999) has recently proposed a revision of the section; in North America this includes *S. collina*, *S. kali*, *S. paulsenii*, *S. tragus* and *S. soda*. Wilken (1993) and Mosyakin (1996) list several names that have been applied or misapplied to *S. tragus* in North America, while Rilke (1999) lists more than fifty synonyms for Old World *S. tragus* alone.

Hybridization between species within this section apparently has occurred in their native range. Intermediate forms, such as between *S. paulsenii* and *S. tragus*, extend over a wide geographic area in central Asia (Rilke 1999, p. 159). Rilke suggested that such zones may occur in North America as well (Rilke 1999, p. 164), although her monograph specifically states that few North American specimens were observed during its preparation. Other authors have also suggested the possibility of interspecific hybridization among *Salsola* species in North America (Arnold 1973; Beatley 1973; Wilken 1993). Experimental evidence, however, was not presented.

Against this background of taxonomic and genetic commotion, there are only a limited number of reliable morphological characters available to distinguish the closely related species of sect. *Salsola* s.l. For example, the most recent *Salsola* treatment for California (Wilken 1993) primarily used tepal-wing presence and diameter, plus stem pubescence, to separate three species in two sections s.s., while Rilke (1999) also used individual tepal-wing dimensions and anther length to separate ten species of subsection *Kali*.

DNA sequence data has also been used to examine phylogenetic relationships in *Salsola*. Pyankov et al. (2002) used the Internal Transcribed Spacer (ITS) of 18S-26S ribosomal DNA, as well as anatomical and physiological characters, to examine 34 *Salsola* and allied species from Europe and Asia. Most-parsimonious analysis of the ITS data grouped *S. kali* and *S. paulsenii* together in a single clade within a multiclade group possessing NADP-malic enzyme C4 photosynthesis, in agreement with analyses of *Salsola* based on anatomical characters (Botschantsev 1969; Freitag 1997). Samples from North America were not examined in that analysis.

To better understand the origins and identities of invasive *Salsola* spp. in North America, genetic variation has been explored to a limited extent with molecular markers. In California, Ryan and Ayres (2000) used isoenzymes and RAPD (Randomly Amplified Polymorphic DNA) markers to examine genetic variation in entities that were then thought to all be *S. tragus*. Two widespread genetic entities were found within the state, distinguished initially by either molecular marker system and tepal-wing width. *Salsola tragus* Type A could be distinguished from *S. tragus* Type B by patterns of aspartate aminotransferase and 6-phosphogluconate dehydrogenase. Isoenzyme patterns were consistent with *S. tragus* Type B being diploid, and *S. tragus* Type A being tetraploid. The RAPD analyses indicated that there was more variation within *S. tragus* Type A than within *S. tragus* Type B. Also, *S. tragus* Type B was characterized by somewhat broader wings on the fruit (Ryan and Ayres 2000). The authors suggested that *S. tragus* Type B was probably a previously unrecognized taxon, due to the large genetic distance between it and *S. tragus* Type A, and their morphological and cytological differences. *Salsola tragus* Type B was thus designated as just Type B from then on.

Accessions of *S. tragus* or *S. kali* from Turkey and France fell within the general *S. tragus* Type A group according to the RAPD analysis (Ryan and Ayres 2000). Also, individuals of *S. paulsenii* were more closely associated with *S. tragus* Type A than with Type B. Later work demonstrated that *S. tragus* from Ukraine showed identical patterns of aspartate aminotransferase and 6-phosphogluconate dehydrogenase as *S. tragus* Type A from California (F. J. Ryan and S. L. Mosyakin, personal observations). RAPD analysis of samples of *S. tragus* from Ukraine (F. J. Ryan and S. L. Mosyakin personal observations) and from Uzbekistan (Sobhian et al. 2003) indicated that these were similar to *S. tragus* Type A from California as well and distinct from Type B.

The inability to determine the origin of Type B is problematic for biological control efforts. *Salsola tragus* and Type B have displayed differential susceptibility to the potential biological control fungus *Colletotrichum gloeosporioides* (Penz.) Penz. and Sacc. in Penz. and the gall midge *Desertovellum stackelbergi* Mamaev (Bruckart et al. 2003; Sobhian et al. 2003; respectively), with Type B being much less affected by either agent. If a biological control agent is effective against one invasive type but not the other, there is potential for the uncontrolled type to increase its range, as happened with ecotypes of *Chondrilla juncea* L. (Burdon et al. 1981). Determining the origin of Type B may assist in locating control agents that are more effective against that entity.

Control of Type B is important, as it is the dominant *Salsola* found in the South Coast Ranges and the foothills of the Transverse and Peninsular Ranges of California. Type B is also common in the southern San Joaquin Valley of California, and while not dominant, it is almost as frequently encountered there as is *S. tragus* (P. Akers personal communication). The distribution of Type B in western North America outside of California and Arizona is unknown, as is the introduction date.

The most recent advance in understanding the identity of Type B came in 2005, when G.F. Hrusa examined a Namibian specimen of *S. kali* subsp. *austroafricana* Aellen (*Seydel 3218*, UC M308692) and noted that it closely matched Type B in all morphological characters (G.F. Hrusa, in prep.).

Molecular markers are a valuable tool for testing hypotheses of relationship and identity based on morphology. Here we use an intron of the nuclear DNA sequence for the enzyme phosphoenolpyruvate carboxylase (PEPC, E.C.4.1.1.31) to: (i) investigate the genetic identity of *S. tragus* in its native range and in North America, (ii) explore the relationships between *S. tragus*, *S. kali* subsp. *austroafricana*, and Type B, and (iii) investigate origins of Type B. This genetic analysis will aid in the development of a biological control strategy for these important weeds.

METHODS

Plant Material

A total of 89 plants were sequenced for the PEPC fourth intron, including *S. soda* (USA, 1

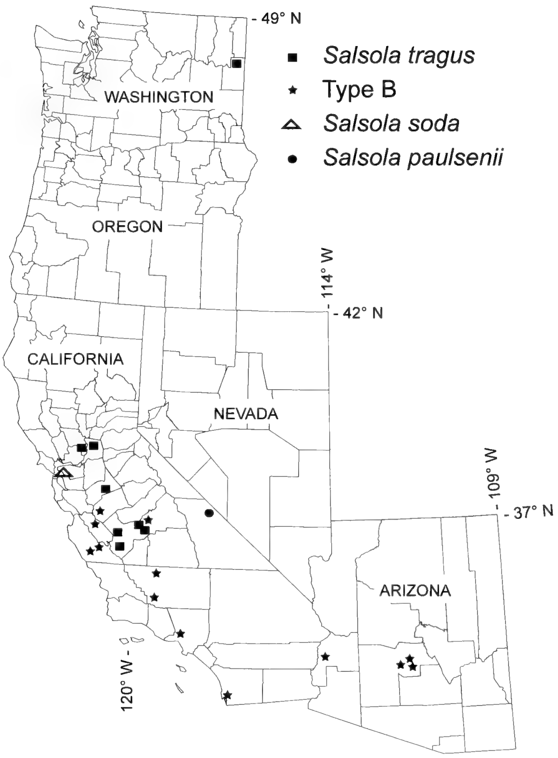

FIG. 1. Map of western USA collections of *Salsola* spp. For many locations more than one plant was collected (see Table 1).

plant), *S. paulsenii* (USA, 2), *S. tragus* (USA, 15; Eurasia, 26; northern Africa, 4), Type B (USA, 33), and *S. kali* subsp. *austroafricana* (southern Africa, 8). More in-depth sampling was used for *S. tragus* and Type B to investigate variation within the invasion (Fig. 1). The number of Old World *S. kali* subsp. *austroafricana* samples included was limited due to its recent inclusion in the study and lack of sample availability. Small branches of dried plants were shipped to Fresno from overseas. Locations of collections, collectors, and voucher information are provided in Table 1. For a few samples, only enough material for DNA extraction was collected, and these have no herbarium voucher. All existing vouchers were deposited at CDA (California Department of Food and Agriculture, Sacramento, CA).

DNA Analysis

Following extraction of DNA by standard methods (as described in Ryan and Ayers 2000), amplification of the intron between the fourth and fifth exon of the PEPC gene utilized the primer pair ppcx4f (5′-ACTCCACAGGATGA-GATGAG-3′) and ppcx5r (5′-GCAGCCAT-CATTCTAGCCAA-3′) designed by J.F. Gaskin from the sequences of other taxa of the Caryophyllales found in GenBank. Amplification was conducted after a 2 min denaturation at 95°C and consisted of 30 cycles of 95°C (1 min), 52°C (1 min) and 72°C (2 min); followed by 5 min at 32°C. The two PCR products (one band approximately 500 bases in length and the other approx. 400 bases in length) were present in all samples. These bands were separated by electrophoresis on a 2% agarose gel and the shorter band was excised (the identity of the longer band is unknown, and its sequence variation was not useful for this analysis). DNA was purified with the Qiagen QIAquick Gel Extraction Kit. The resultant template was sequenced on a Beckman CEQ 2000XL using reagents and protocols supplied by the manufacturer and the same primers mentioned above. Each heterozygotic genotype was cloned and sequenced to determine the haplotypes involved. Clones were created using the Promega pGEM-T Vector System II, then sequenced using the protocol above. Sequences were aligned by hand using SE-Al software (Rambaut 1996) and are available in GenBank (accession numbers are in Table 2). Haplotypes were arranged manually into a most parsimonious network (Fig. 2). Measures of haplotype diversity were based on the formula $h = (1 - \sum x_i^2)\, n/(n - 1)$, where x_i is the frequency of a haplotype and n is the sample size (Nei and Tajima 1981).

Results and Discussion

DNA Sequences of *Salsola* spp.

The PEPC intron marker for taxa in this study is 394 to 396 bases in length, with 38 (9.6%) variable bases. Plant samples contained one or two discernable copies of the marker (homozygous or heterozygous, respectively). The most parsimonious network (Fig. 2), excluding the outgroup *S. soda*, contained 13 mutations with no homoplasy (i.e., no mutations had to be placed in more than one position in the network). All mutations were single nucleotide changes (no insertion-deletion events). *Salsola soda* was 25 mutational steps (23 single nucleotide changes and two insertion-deletion events) away from the cluster formed by the relatively closely related *S. tragus*, *S. kali* subsp. *austroafricana*, *S. paulsenii* and Type B.

For the 88 samples of *S. tragus, S. kali* subsp. *austroafricana, S. paulsenii* and Type B that were sequenced, we found 11 haplotypes in 15 different genotypic combinations (Table 1). Only two samples of *S. paulsenii* were examined and they each contained genotypes 1/7. This combination was not found in any other taxon sampled. The most common genotypes within *S. tragus* were 2/5 (40%) and 1/2 (28%). Both genotypes were found in Eurasia, northern Africa, and the USA.

TABLE 1. MORPHOLOGICAL AND GENOTYPIC DESCRIPTION OF SPECIMENS USED IN STUDY OF *SALSOLA*. * indicates that herbarium voucher does not exist.

Species or type	Continent	Country or U.S. state	City or location	Plant DNA #	PEPC genotype	Collector	Date of collection
S. tragus	Africa	Tunisia	Kasserine	S4-14	1/6	R. Sobhian	1-Sep-1998
S. tragus	Africa	Tunisia	Bengaden	S4-13	2/5	R. Sobhian	31-Aug-1998
S. tragus	Africa	Tunisia	Sousse	S9-43	2/11	R. Sobhian	22-Aug-1998
S. tragus	Africa	Tunisia	Sfax	S9-44	9/11	R. Sobhian	30-Aug-1998
S. tragus	Asia	China	Beijing	S4-04	9/9	R. Sobhian	25-Jul-1997
S. tragus	Asia	China	Tang Shan	S4-02	10/10	R. Sobhian	30-Jul-1997
S. tragus	Asia	China	Tang Shan	S4-03	10/10	R. Sobhian	30-Jul-1997
S. tragus	Asia	Kazakhstan	Taraz	S9-9	1/1	R. Sobhian	10-Aug-1998
S. tragus	Asia	Kazakhstan		S4-11*	1/2	R. Sobhian	1-Aug-1998
S. tragus	Asia	Kazakhstan		S6-40	1/2	L. Fornaseri	
S. tragus	Asia	Kazakhstan	S. of Cimkent	S4-10	2/5	R. Sobhian	5-Dec-1998
S. tragus	Asia	Pakistan	Warsal	S6-42	1/2	R. Sobhian	5-Aug-1998
S. tragus	Asia	Pakistan	Chashma	S9-41	1/12	R. Sobhian	5-Dec-1998
S. tragus	Asia	Uzbekistan	Sherobod	S4-5	2/5	R. Sobhian	22-Jun-1997
S. tragus	Asia	Uzbekistan	Bukhara	S4-7	2/5	R. Sobhian	24-Jun-1997
S. tragus	Europe	France	Grau du Roi	S9-15	1/2	R. Sobhian	6-Sep-1995
S. tragus	Europe	France	Carnon	S4-17	2/5	R. Sobhian	13-Oct-1995
S. tragus	Europe	Turkey	Aydincik	S6-38	1/2	R. Sobhian	27-May-1997
S. tragus	Europe	Turkey	Isparta	S8-24	1/2	R. Sobhian	14-Sep-1995
S. tragus	Europe	Turkey	Finike	S4-1	2/5	R. Sobhian	11-Sep-1997
S. tragus	Europe	Turkey	Isparta	S8-23	2/5	R. Sobhian	1-Oct-1995
S. tragus	Europe	Turkey	Aydincik	S9-37	2/5	R. Sobhian	27-May-1997
S. tragus	Europe	Turkey	Kirka	S8-22	2/6	R. Sobhian	13-Sep-1995
S. tragus	Europe	Ukraine	Genichesk Dist.	2003	2/2	I. I. Moisienko	17-Oct-2000
S. tragus	Europe	Ukraine	Gola Prystan'	2007	2/2	O. Y. Umanets	15-Oct-2000
S. tragus	Europe	Ukraine	Kiev	2000	2/5	S. Mosyakin	14-Sep-2000
S. tragus	Europe	Ukraine	Kiev	2001*	2/5	O. S. Sakun	14-Sep-2000
S. tragus	Europe	Ukraine	Gladkovka	2002	2/5	O. Y. Umanets	17-Oct-2000
S. tragus	Europe	Ukraine	Tsyurupinsk	2004	2/5	O. Y. Umanets	17-Oct-2000
S. tragus	Europe	Ukraine	Tsyurupinsk	2005	2/5	O. Y. Umanets	17-Oct-2000
S. tragus	N. America	CA	Davis	372	1/2	F. Ryan	11-Oct-1999
S. tragus	N. America	CA	Fresno	373*	1/2	F. Ryan	20-Apr-1997
S. tragus	N. America	CA	Coalinga	375	1/2	F. Ryan	23-Oct-1999
S. tragus	N. America	CA	Sacramento	4135	1/2	P. Akers RT05-3	18-Sep-2002
S. tragus	N. America	CA	Turlock	4137	1/2	P. Akers RT42-3	11-Nov-2002
S. tragus	N. America	CA	Kamm Rd./I-5	S8-19*	1/2	F. Ryan	
S. tragus	N. America	CA	Kamm Rd./I-5	S8-20*	1/2	F. Ryan	
S. tragus	N. America	CA	Fresno	374	2/2	F. Ryan	1-Oct-1999
S. tragus	N. America	CA	Davis	4132	2/5		1-Sep-2000
S. tragus	N. America	CA	Parlier	4133	2/5	P. Akers RT 14-01	23-Sep-2002
S. tragus	N. America	CA	Turlock	4136	2/5	P. Akers RT 42-01	11-Nov-2002
S. tragus	N. America	CA	Kamm Rd./I-5	S4-18*	2/5	F. Ryan	
S. tragus	N. America	WA	Spokane	S6-45	1/2	D. Ayres	11-Aug-1998
S. tragus	N. America	WA	Spokane	S9-46	2/5	D. Ayres	11-Aug-1998
S. tragus	N. America	WA	Spokane	S9-48	2/11	D. Ayres	11-Aug-1998
Type B	N. America	AZ	Avondale	6061	3/3	D. Ayres	28-Dec-1998
Type B	N. America	AZ	Phoenix	6064	3/3	D. Ayres	27-Dec-1998
Type B	N. America	AZ	Phoenix	6065	3/3	D. Ayres	27-Dec-1998
Type B	N. America	AZ	Phoenix	6067	3/3	D. Ayres	27-Dec-1998
Type B	N. America	AZ	Phoenix	S8-25	3/3	D. Ayres	27-Dec-1998

TABLE 1. CONTINUED.

Species or type	Continent	Country or U.S. state	City or location	Plant DNA #	PEPC genotype	Collector	Date of collection
Type B	N. America	AZ	Phoenix	S8-26	3/3	D. Ayres	27-Dec-1998
Type B	N. America	AZ	Tempe	S9-49	3/3	D. Ayres	27-Dec-1998
Type B	N. America	AZ	Phoenix	6066	3/4	D. Ayres	27-Dec-1998
Type B	N. America	AZ	Avondale	6060	4/4	D. Ayres	28-Dec-1998
Type B	N. America	AZ	Avondale	6062	4/4	D. Ayres	28-Dec-1998
Type B	N. America	AZ	Avondale	6063	4/4	D. Ayres	28-Dec-1998
Type B	N. America	AZ	Quartzite	S9-31	4/4	D. Ayres	28-Dec-1998
Type B	N. America	AZ	Avondale	S9-35	4/4	D. Ayres	28-Dec-1998
Type B	N. America	AZ	Quartzite	S9-36	4/4	D. Ayres	28-Dec-1998
Type B	N. America	CA	Fresno	376	3/3	F. Ryan	21-Jul-1997
Type B	N. America	CA	Famoso	4142	3/3	P. Akers RT74-01	1-Oct-2002
Type B	N. America	CA	San Diego	S9-54	3/3	F. Ryan	5-Nov-1999
Type B	N. America	CA	Maricopa	6140.00	3/3	G.F. Hrusa 16172	12-Oct-2003
Type B	N. America	CA	Paicines	6144.00	3/3	G.F. Hrusa 16186	14-Oct-2003
Type B	N. America	CA	Lockwood	6145.00	3/3	G.F. Hrusa 16193	14-Oct-2003
Type B	N. America	CA	San Lucas	6151.00	3/3	G.F. Hrusa 16183a	13-Oct-2003
Type B	N. America	CA	San Lucas	6154.00	3/3	G.F. Hrusa 16183d	13-Oct-2003
Type B	N. America	CA	Fresno	377	4/4	F. Ryan	20-Apr-1997
Type B	N. America	CA	Santa Nella	378*	4/4	F. Ryan	
Type B	N. America	CA	CA 152, Merced Co.	4140	4/4	P. Akers RT13-01	23-Sep-2002
Type B	N. America	CA	CA 152/ I-5	4141	4/4	P. Akers RT30-02	10-Oct-2002
Type B	N. America	CA	Santa Nella	S9-52*	4/4	D. Ayres	
Type B	N. America	CA	Santa Nella	S9-53*	4/4	D. Ayres	
Type B	N. America	CA	Calabasas	6168.00	4/4	B. Villegas 247-1	21-Aug-2002
Type B	N. America	CA	Calabasas	6169.00	4/4	B. Villegas 247-2	21-Aug-2002
Type B	N. America	CA	Calabasas	6170.00	4/4	B. Villegas 247-3	21-Aug-2002
Type B	N. America	CA	Calabasas	6171.00	4/4	B. Villegas 247-4	21-Aug-2002
Type B	N. America	CA	Calabasas	6172.00	4/4	B. Villegas 247-5	21-Aug-2002
S. kali subsp. *austroafricana*	Africa	South Africa	Robertson	6068	3/3	S. Neser	
S. kali subsp. *austroafricana*	Africa	South Africa	Robertson	6069	3/3	S. Neser	
S. kali subsp. *austroafricana*	Africa	South Africa	Vioolsdrift	6070	3/3	S. Neser	
S. kali subsp. *austroafricana*	Africa	South Africa	Vioolsdrift	6071	3/3	S. Neser	
S. kali subsp. *austroafricana*	Africa	Namibia	Windhoek	6797	3/3	A. Kirk & C. Pickett	5-Sep-2005
S. kali subsp. *austroafricana*	Africa	South Africa	Kimberly #3	6800	3/3	M. Rejmanek	
S. kali subsp. *austroafricana*	Africa	South Africa	Kimberly	6802	3/3	M. Rejmanek	28-Oct-2005
S. kali subsp. *austroafricana*	Africa	South Africa	Kimberly	6803	3/3	M. Rejmanek	28-Oct-2005
S. paulsenii	N. America	CA	Eureka Valley	Eureka 3	1/7	F. Ryan	28-Dec-2001
S. paulsenii	N. America	CA	Eureka Valley	Eureka 4	1/7	F. Ryan	28-Dec-2001
S. soda	N. America	CA	Berkeley	4160	15/15	F. Ryan	13-Aug-1998

TABLE 2. GENBANK ACCESSION NUMBERS FOR *SALSOLA* SPP. HAPLOTYPES.

PEPC haplotype	GenBank accession number
1	DQ257378
2	DQ005542
3	DQ257379
4	DQ005543
5	DQ005544
6	DQ257380
7	DQ257381
9	DQ257382
10	DQ257383
11	DQ257384
12	DQ257385
15	DQ257386

The most common *S. tragus* genotype among the USA specimens was 1/2 (53%), which was found both in the central valley of California and in Spokane, WA. The 1/2 genotype was found in Turkey, Kazakhstan, Pakistan, and presumably in intermediate localities while 2/5 was found in Tunisia, Turkey, Kazakhstan, Uzbekistan, and Ukraine. Due to the widespread distribution in the native range of the genotypes found in the USA, conclusions cannot be drawn concerning the native source of introduced *S. tragus*.

The haplotypes found in *S. tragus*, *S. kali* subsp. *austroafricana*, Type B, and *S. paulsenii* are all relatively closely clustered on the haplotype network (Fig. 2) when compared to the

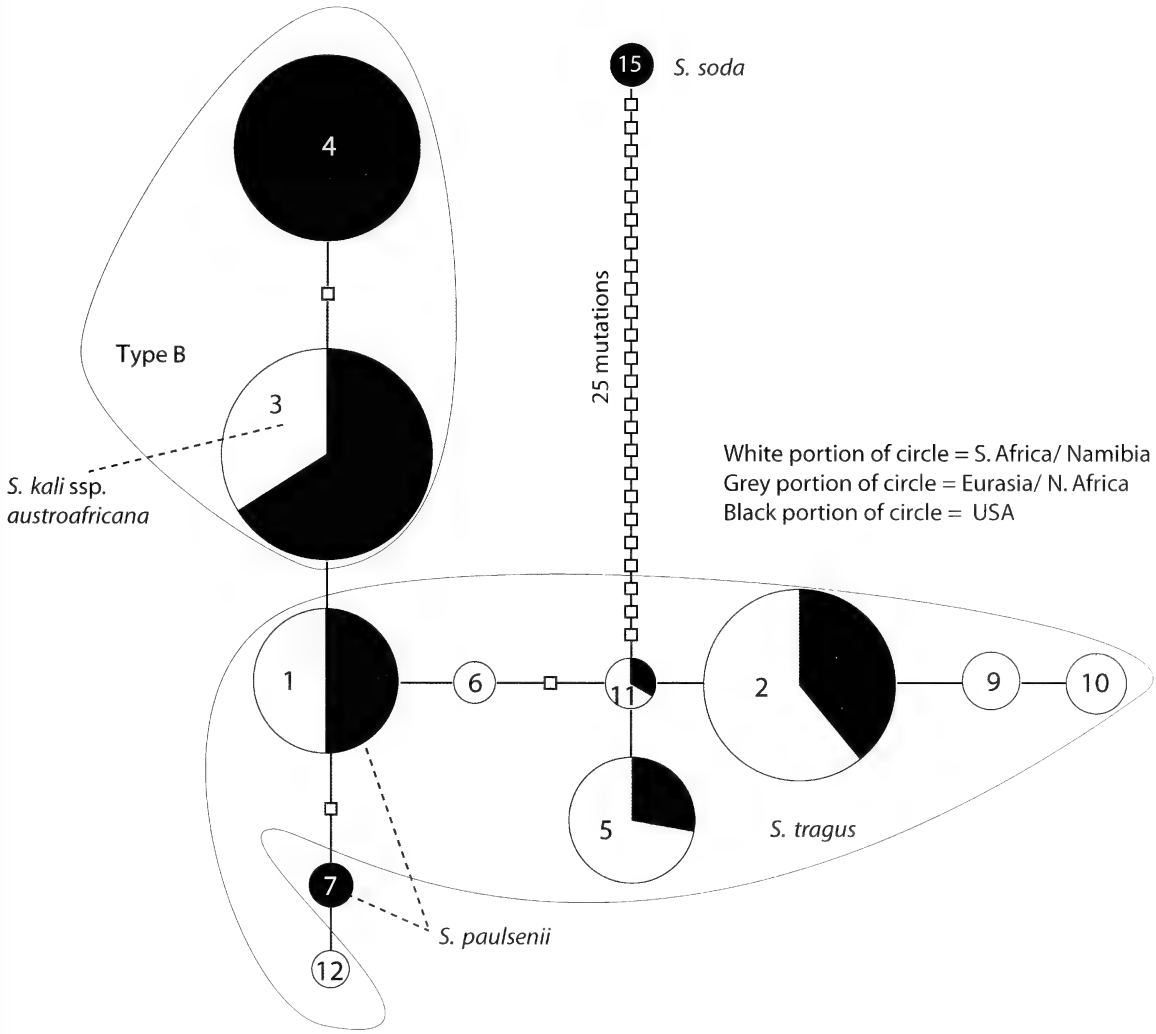

FIG. 2. Haplotype network of DNA sequences of the fourth intron of the PEPC gene region for 89 samples of *Salsola* species from the USA, Africa and Eurasia. Circles represent haplotypes recovered, and squares along lineages in between circles indicate haplotypes not recovered. Size of a circle is proportionate to haplotype frequency worldwide. The pie slices of a circle indicate the percentage of haplotypes from the USA (black), Eurasia/ N. Africa (gray), and southern Africa (white). Each link between haplotypes indicates one mutational event. Angle of bifurcation and length of link between haplotypes have no significance. The loops that surround portions of the haplotype network indicate taxonomic status of plant collections sampled.

mutational distance to the congener *S. soda*. *Salsola tragus* and *S. paulsenii* share haplotype 1, which may be due to incomplete lineage sorting or hybridization, either of which suggests a close relationship of the two species. The native ranges of *S. tragus* and *S. paulsenii* overlap and morphological hybrids appear to be present (Rilke 1999). Further analysis could investigate if putative hybrid combinations in the USA and native range are genetically similar, or if novel hybrid genotypes have been created in the USA since the introduction of the two species, which has happened in other taxa (e.g., Ellstrand and Schierenbeck 2000; Gaskin and Schaal 2002).

Haplotype diversity was larger in the *S. tragus* invasion compared to the Type B invasion in the USA (h = 0.739 vs. 0.506 respectively). Levels of observed heterozygosity varied greatly between invasive samples from the two taxa, with H_o = 0.84 in *S. tragus* compared to H_o = 0.03 in Type B. These results are consonant with *S. tragus* being tetraploid (2N = 36), and Type B being a diploid species (2N = 18) which is supported by the isoenzyme patterns as well (Ryan and Ayres 2000), but could also be influenced by the founding event(s). Each of the Type B genotypes appeared to be quite widespread, in agreement with initial observations of a low amount of genetic variation in comparison with *S. tragus* (Ryan and Ayres 2000).

The interaction of biological control agents with different *S. tragus* genotypes has not been examined. Preliminary host-specificity results with *Colletotrichum gloeosporioides* (Bruckart et al. 2003) and *Desertovellum stackelbergi* (Sobhian et al. 2003) indicate that plant genotype may be a factor in certain *Salsola* control scenarios. Though distinct genotypes of invasives may not correlate with the phenotypic characters that influence behavior of biological control agents (see Reed and Frankham 2001), there are examples of intraspecific genetic variation of weeds affecting insect herbivory in other systems (Karban and Kittelson 1999; Herrin and Warnock 2002). Inclusion of a variety of invasive *S. tragus* genotypes in biological control agent host-specificity tests, compared to using material from just one or a few stock individuals, will extend our understanding of how agents might be effective across the range of the invasion.

Analysis of *S. tragus* and Type B with the PEPC intron marker confirms the earlier morphological, cytological, isoenzymic, and RAPD results supporting *S. tragus* and Type B as distinct entities. The recent inclusion of *S. kali* subsp. *austroafricana* from southern Africa in our studies provides the first match with Type B using either morphology or DNA. Although it is possible that other *Salsola* taxa in the Old World may also possess the same haplotypes as Type B, the concurrent morphological and molecular matches indicate that California and Arizona's Type B is indeed the plant described as *S. kali* subsp. *austroafricana*. Haplotype 4 of Type B still does not match with any Old World specimens, and further sampling needs to be done on *S. kali* subsp. *austroafricana* in southern Africa to determine if genotype 3/3 is dominant in the subspecies. *Salsola kali* subsp. *austroafricana* has also been reported from Australia (Rilke 1999), but no specimens were cited and it has not been recently confirmed from there.

Salsola sect. *Kali* (which includes *S. kali* subsp. *austroafricana*) has usually been assumed introduced in southern Africa, as the section is thought to be native only in the northern hemisphere. Botschantsev (1974) treated *S. kali* ssp. *austroafricana* as a synonym of *S. australis* R.Br. (=*S. tragus* L.) and stated that these were adventive in south and southwest Africa. Rilke (1999) also considered section *Kali* introduced in the southern Africa region. However, given the specific epithet, this position must not have been universal among all botanists. Perusal of large European and Asian herbaria (LE, KW, and MPU) by Ukrainian and USDA collaborators, and the accounting by Rilke, have not revealed specimens from outside of southern Africa that are morphologically similar to *S. kali* ssp. *austroafricana*. Known native *Salsola* in southern Africa are not closely related to the *S. tragus* complex (Botschantsev 1974) and a single intraspecific level hemispheric disjunct, particularly of a weedy plant, would seem unusual. However, given its apparent absence in European and Asian collections, it cannot be stated with absolute confidence that the plant is introduced in southern Africa. Further study would appear necessary before this question can be answered.

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TWO DECADES OF CHANGE IN DISTRIBUTION OF EXOTIC PLANTS AT THE DESERT LABORATORY, TUCSON, ARIZONA

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ABSTRACT

A gridline survey for exotic plant species was undertaken in 1983 and repeated in 2005 at the Desert Laboratory, a 352-ha natural area just west of downtown Tucson, Arizona, USA. Coordinate data gathered during the surveys were used to plot distributions, determine frequencies (number of coordinate locations), and assess percent change. Fifty-two exotic species were encountered in all, 34 in the first survey, 44 in the second. The proportion of ornamental exotics doubled over time, reaching 50% in 2005. Casual, naturalized, and invasive exotics comprised 44%, 40%, and 15% of species found during the surveys. Minimum residence time increased significantly from casual to naturalized to invasive species, suggesting that the longer a species was present, the more likely it was to surmount barriers to naturalization and invasion. In both 1983 and 2005, casual, naturalized, and invasive species differed in mean frequency by an order of magnitude, with casual species having the lowest frequencies and invasive species the highest. Between surveys, frequency of 18 species decreased; most other species increased in frequency. The recent surge in ornamental exotics, combined with temporal trends in invasiveness, indicates that the proportion of invasive species in the flora will increase with time.

Key Words: alien plants, distribution maps, invasions, nonnative species, Sonoran Desert.

That invasive exotics can irreversibly change natural ecosystems is indisputable (Mack et al. 2000; Levine et al. 2003), but despite all that has been learned in recent years about the autecology and synecology of plants established outside their native range, ecologists and land managers have difficulty predicting which species will become invasive (Mack et al. 2000; Kolar and Lodge 2001). This difficulty results in part from lack of detailed historical information about change in distribution over time (Mack et al. 2000; Hunter and Mattice 2002). When spatial coverage of exotics can be measured, change in area over time can be used to describe rate of spread according to simple reaction-diffusion models (Frappier et al. 2003) or more complex lag-phase models (Mack et al. 2000). Although maps showing the local distribution of exotic species at a single point in time (e.g., Agius 2003) have become increasingly common, repeated mapping of exotic distributions at the local scale is still relatively rare. One notable example is the use of aerial photographs to map distribution of *Phragmites australis* in nine years between 1945 and 1999 (Wilcox et al. 2003). More commonly, changing distributions of exotics have been assessed by repeated censuses of vegetation plots (e.g., Daehler and Carino 1998; Johnstone et al. 1999) or by repeated inventories within local areas (e.g., Hunter and Mattice 2002). Here we present results from two gridline surveys for exotic plants in a 352-ha natural area in the northern Sonoran Desert, USA. The surveys, made in 1983 and 2005, allowed us to map local distributions of 52 exotic species and assess changes in distribution over 22 years.

Our study site, the Desert Laboratory, was founded as a botanical research station in 1903. It is unique among natural areas in the Sonoran Desert for having been protected from domestic livestock for almost 100 years and for its long and distinguished record of ecological research (White 1985). The Desert Laboratory grounds were colonized by exotics as long ago as 1906 (Spalding 1909). From a total of four species in 1909, the exotic flora increased to 52 species by 1991 (Burgess et al. 1991). Most exotics at our study site were introduced to the Sonoran Desert region from the Old World or Latin America (Wilson et al. 2002). A few species were introduced as ornamental plants from elsewhere in the United States. Exotics of particular concern include winter-annual grasses, especially *Bromus rubens, Schismus arabicus*, and *S. barbatus*, and two perennial grasses, *Pennisetum ciliare* and *P. setaceum. Bromus rubens* and *P. ciliare* can form a continuous cover of light fuels, increasing fire frequency and severity in desertscrub communities where plants are not adapted to burning (Esque and Schwalbe 2002; Búrquez-Montijo et al. 2002). *Bromus rubens* and *Schismus* spp. significantly reduce the density and biomass of native winter annuals; over the long term, they could also reduce native seed banks, bringing about fundamental alterations in plant community structure and food web dynamics (Brooks

2000; Salo et al. 2005). *Pennisetum setaceum* has the potential to displace native species and promote fire (Wilson et al. 2002). These species are all *transformers*, defined as invasive exotics that "change the character, condition, form or nature of ecosystems over a substantial area" (Richardson et al. 2000).

In spring 1983, we undertook a survey of exotic plants on the Desert Laboratory grounds by walking regular gridlines and recording Cartesian coordinates of exotic species (Burgess et al. 1991). In spring 2005, native and exotic annuals were abundant after a relatively wet winter (precipitation = 151 mm), making it worthwhile to repeat the initial survey, which was undertaken after an unusually wet winter (precipitation = 250 mm). Burgess et al. (1991) discussed geographic origins and breeding systems of invasive exotics found during the original survey and also described the environmental and cultural factors that promoted invasion. Our objectives for the second survey were to: (1) map the distribution of individual exotic species in 2005, (2) use mapped distributions to categorize exotics as casual, naturalized, or invasive, (3) assess changes in distribution and frequency between 1983 and 2005, and (4) identify priorities for monitoring and eradication.

Here and throughout, we have followed the terminology of Richardson et al. (2000) except for our use of the term *exotic* instead of *alien* and for minor modifications to suit the temporal and spatial scales of our study. We defined *exotic* as non-native in the vicinity of Tucson; we needed an unusually narrow definition because several species that are indigenous to Arizona but not to the vicinity of Tucson have spread onto our study site from ornamental plantings in nearby neighborhoods. *Casual exotic plants* are species that have not formed self-replacing populations but rather depend on repeated introduction for their persistence (Richardson et al. 2000). *Naturalized exotics* reproduce consistently and sustain populations over many life cycles, typically recruiting close to the parent plants. Although often associated with disturbance, naturalized exotics are not necessarily restricted to disturbed sites (Richardson et al. 2000). *Invasive exotics* are naturalized species that produce large numbers of offspring at considerable distances from the parents and thus can spread over wide areas in relatively short times, often including successionally mature, undisturbed communities; for taxa spreading by seed, the scale of movement is >100 m during <50 years (Richardson et al. 2000). Because we seldom knew the original place or time of introduction for most exotics on our study area, we used a more qualitative assessment to distinguish between naturalized and invasive exotics: naturalized exotics are self-replacing species most likely to be found on disturbed sites or, if more widely distributed, having small populations at the local scale, whereas invasive exotics are self-replacing species that are ubiquitous and abundant in undisturbed communities. Our modifications retain an important distinction, which is that invasive species have overcome environmental barriers to widespread dispersal and proliferation (Richardson et al. 2000).

Methods

Study Area

The Desert Laboratory (32°13′N, 111°00′W) is a 352-ha research station and natural area situated west of downtown Tucson, Arizona, USA. The laboratory grounds include Tumamoc Hill, a rocky, basaltic-andesitic knoll (760 to 948 m above sea level), and the level or gently rolling plain to the west (725 to 760 m above sea level). Housing developments, schools, and businesses border upon the Desert Laboratory to the north, south, and west. A small desert park lies on the eastern boundary. Mean maximum and minimum daily temperatures at Tucson are 18.6°C and 2.4°C during January, the coldest month, and 37.9°C and 22.8°C in June, the hottest month (Sellers et al. 1985). Mean annual rainfall at the Desert Laboratory is 300 mm per year. On average, half the yearly total comes during summer (July through September, 152 mm); most of the remainder falls during winter (November through March, 109 mm). The vascular flora of the study area comprises 346 species, subspecies, and varieties, of which 15% are exotic (Bowers and Turner 1985; Burgess et al. 1991). Study site vegetation is typical of the Arizona Upland subdivision of the Sonoran Desert (Shreve 1951). Dominant native plants include *Parkinsonia microphylla, Carnegiea gigantea, Larrea tridentata, Acacia constricta, Ambrosia deltoidea*, and *Encelia farinosa*. Nomenclature follows Kartesz (1999) insofar as possible.

Status as an ecological reserve has not protected the Desert Laboratory grounds from localized disturbance, starting with construction of laboratory buildings, an access road, and a water system in the early 1900s. Before the grounds were fenced in 1907, wagons carted away surface rock for construction, and cattle, horses, goats, and burros grazed the slopes and flats. After 1907, disturbance was minimal until the 1950s, when easements were granted for construction of petroleum and natural gas pipelines, electric transmission lines, and radio towers. Two clay quarries were dug at some point, and one was used as a landfill in the 1960s. More recently, the petroleum pipeline that crosses the center of the property was replaced (January 2004), as was a portion of the natural gas pipeline that crosses the northeast corner (October 2003).

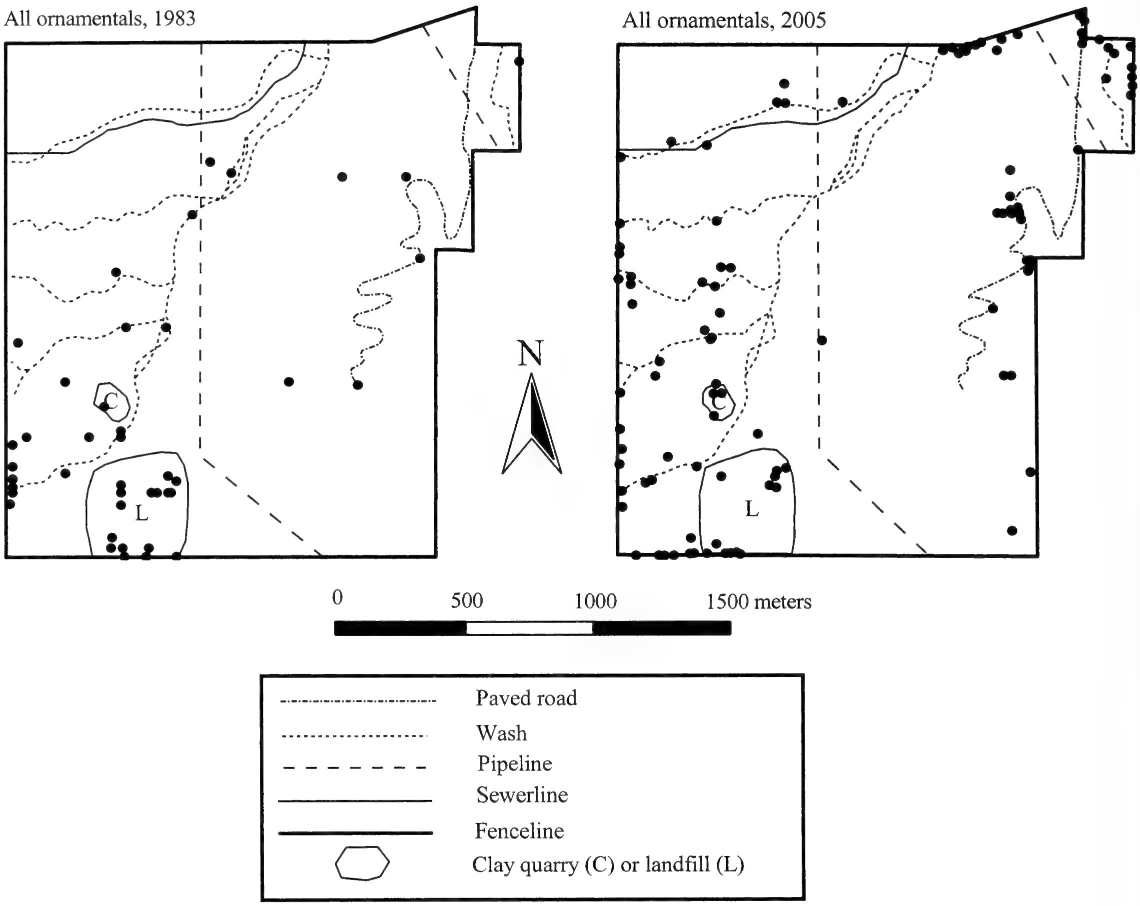

FIG. 1. Distribution of all ornamental species at the Desert Laboratory, Tucson, Arizona, in 1983 and 2005.

Data Collection

We mapped distribution of exotic species within the Desert Laboratory boundaries in spring 1983 and again in spring 2005. In 1983, we drew a grid of parallel lines on aerial photographs (scale 1:2256) of the study site, then walked each gridline, using the aerial photographs to maintain as accurate a course as possible (Burgess et al. 1991). We also surveyed the paved road and the fenceline that is the boundary of the study site. As we encountered exotic plants, we recorded their Cartesian coordinates within about two meters of the gridline. Distance between coordinate locations varied widely but averaged about 44 m. The gridlines were about 220 m apart and had a total length of about 40 km. In 2005, we repeated the survey on the same gridlines but used a hand-held GPS unit instead of aerial photographs to keep ourselves on course. Every 30 to 40 meters, we recorded latitude and longitude as a GPS waypoint. As we encountered exotic species, we assigned them to the most recent waypoint. We recorded more coordinate locations in 2005 ($n = 1349$) than in 1983 ($n = 976$). For convenience, we pooled certain morphologically similar species, treating *Schismus arabicus* and *Schismus barbatus* as *Schismus* spp. and *Sonchus asper* and *Sonchus oleraceus* as *Sonchus* spp.

Data Analysis

The scattered distribution of many species across our study site made it difficult to draw discrete polygons showing areal extent or to calculate rate of spread in meters per year. Instead, we depicted distribution as dot maps from which we determined frequency of observation in 1983 and 2005. Specifically, we used ArcView 3.0a to generate a distribution map for each species found at more than five coordinate locations in either year. For every species, we determined frequency as number of coordinate locations where it was recorded in 1983 or 2005, then determined percent change between years as ([frequency in 2005 – frequency in 1983]/frequency in 1983) × 100%. From mapped distributions and our own observations of reproductive behavior and demography, we followed criteria

TABLE 1. FREQUENCY (NUMBER OF COORDINATE LOCATIONS) OF CASUAL EXOTIC PLANTS AT THE DESERT LABORATORY, TUCSON, ARIZONA. Life forms as follows: AF = annual forb, AG = annual graminoid, LS = leaf succulent, PG = perennial graminoid, SH = shrub, SS = stem succulent, TR = tree, O = ornamental. Arrival = year when first reported from Desert Laboratory grounds. Percent change = ([frequency in 2005 − frequency in 1983]/frequency in 1983) × 100%.

Species	Life form	Arrival	Frequency		
			1983	2005	% change
Agave americana	LS, O	1985	0	2	—
Agave murpheyi	LS, O	1987	0	3	—
Aloe sp.	LS, O	2005	0	1	—
Aloe vera	LS, O	2005	0	2	—
Castalis tragus	AF, O	1978	17	7	−58.5
Centaurea melitensis	AF	1983	4	6	50.0
Chenopodium album	AF	1983	4	0	−100.0
Chenopodium murale	AF	1983	1	1	0.0
Lantana urticoides	SH, O	1983	1	3	200.0
Lepidium oblongum	AF	1983	4	0	−100.0
Melia azederach	TR, O	1983	1	0	−100.0
Molucella laevis	AF, O	1983	2	0	−100.0
Nicotiana glauca	SH, O	1983	2	0	−100.0
Olea europaea	TR, O	2005	0	1	—
Opuntia basilaris	SS, O	2005	0	2	—
Opuntia ficus-indica	SS, O	2005	0	1	—
Opuntia microdasys	SS, O	1984	0	3	—
Opuntia santa-rita	SS, O	2005	0	1	—
Polypogon monspeliensis	AG	1978	3	0	−100.0
Prosopis sp.	TR, O	2005	0	2	—
Rumex crispus	AF	1983	1	0	−100.0
Sisymbrium altissimum	AF	1983	4	0	−100.0
Tamarix aphylla	TR, O	2005	0	2	—

in Richardson et al. (2000) to categorize the status (casual, naturalized, or invasive) of each species. From published records (Spalding 1909; Bowers and Turner 1985; Burgess et al. 1991), we determined when each species was first reported from the Desert Laboratory, then calculated minimum residence time after Castro et al. (2005) by subtracting year of first report from

TABLE 2. FREQUENCY (NUMBER OF COORDINATE LOCATIONS) OF NATURALIZED PLANTS AT THE DESERT LABORATORY, TUCSON, ARIZONA. See Table 1 for explanation of column headings.

Species	Life form	Arrival	Frequency		
			1983	2005	% change
Avena fatua	AG	1983	15	26	73.3
Brassica tournefortii	AF	1978	27	66	144.4
Bromus catharticus	AG	1968	7	23	228.6
Caesalpinia gilliesii	SH, O	1989	0	1	—
Cynodon dactylon	PG, O	1909	19	18	−5.3
Cyperus involucratus	PG, O	1985	0	2	—
Eragrostis echinochloidea	PG	2005	0	12	—
Eragrostis lehmanniana	PG	1983	20	8	−60.0
Lactuca serriola	AF	1983	31	27	−12.9
Malva parviflora	AF	1978	6	5	−16.7
Matthiola longipetala	AF, O	1978	16	35	118.8
Melilotus indicus	AF	1983	7	21	200.0
Opuntia engelmannii var. *linguiformis*	SS, O	1985	0	15	—
Parkinsonia aculeata	TR, O	1968	8	20	150.0
Pennisetum setaceum	PG, O	1983	0	33	—
Phalaris minor	AG	1978	3	3	0.0
Rhus lancea	TR, O	1984	0	16	—
Salsola tragus	AF	1968	54	30	−44.4
Sonchus asper, S. oleraceus	AF	1983	63	58	−7.9
Tamarix chinensis	TR, O	1968	3	6	100.0

TABLE 3. FREQUENCY (NUMBER OF COORDINATE LOCATIONS) OF INVASIVE PLANTS AT THE DESERT LABORATORY, TUCSON, ARIZONA. See Table 1 for explanation of column headings.

Species	Life form	Arrival	Frequency		
			1983	2005	% change
Bromus rubens	AG	1968	355	170	−52.1
Erodium cicutarium	AF	1906	440	392	−10.9
Herniaria hirsuta subsp. *cinerea*	AF	1985	0	92	—
Hordeum murinum	AG	1906	211	115	−45.5
Pennisetum ciliare	PG	1968	6	485	7983.3
Schismus arabicus, S. barbatus	AG	1968	763	1067	39.8
Sisymbrium irio	AF	1968	424	511	20.5

the year of the second survey. We used a Kruskal-Wallis test to determine whether average residence time differed among categories (casual, naturalized, invasive). We also used Kruskal-Wallis tests to determine whether categories differed in frequency within years.

RESULTS AND DISCUSSION

Changes in the Exotic Flora

Altogether, we found 52 exotic species during the two surveys. Of these, four species (*Agave*

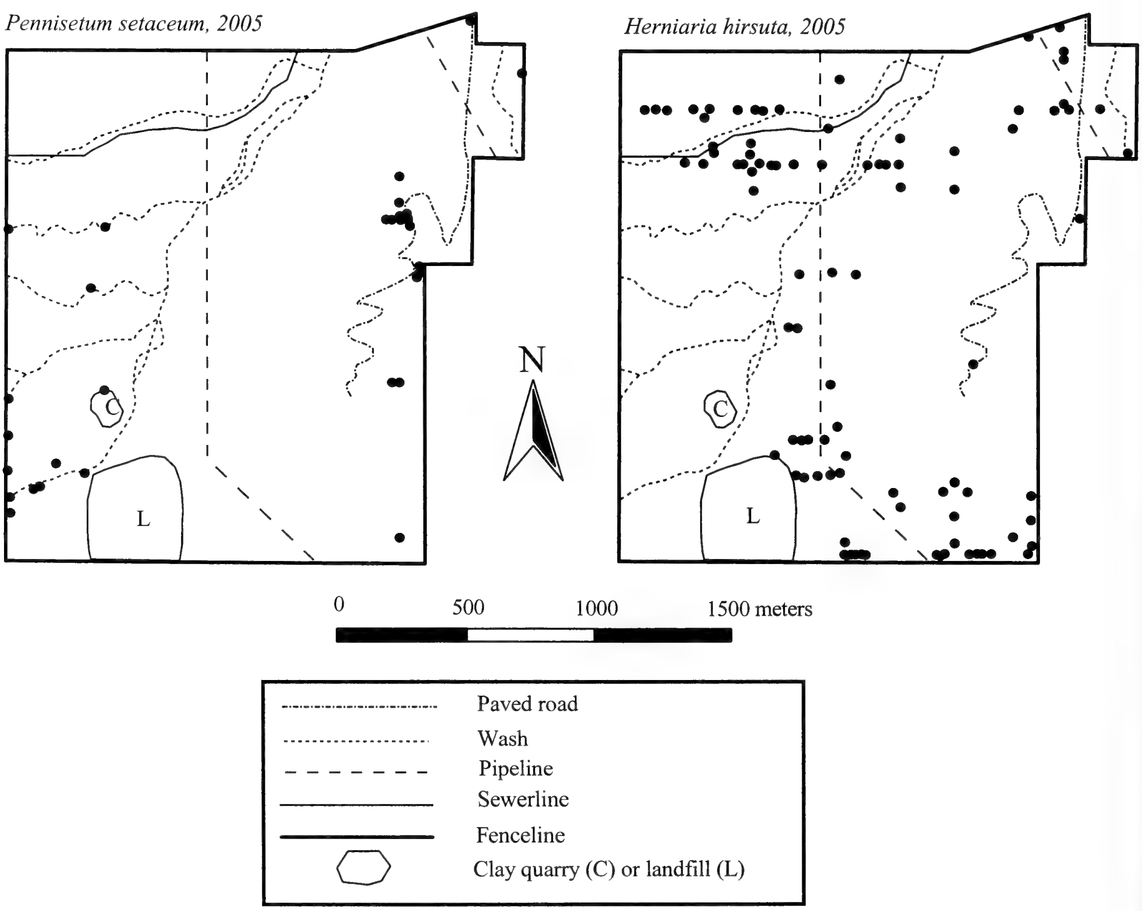

FIG. 2. Distribution of *Pennisetum setaceum* and *Herniaria hirsuta* at the Desert Laboratory, Tucson, Arizona, in 2005.

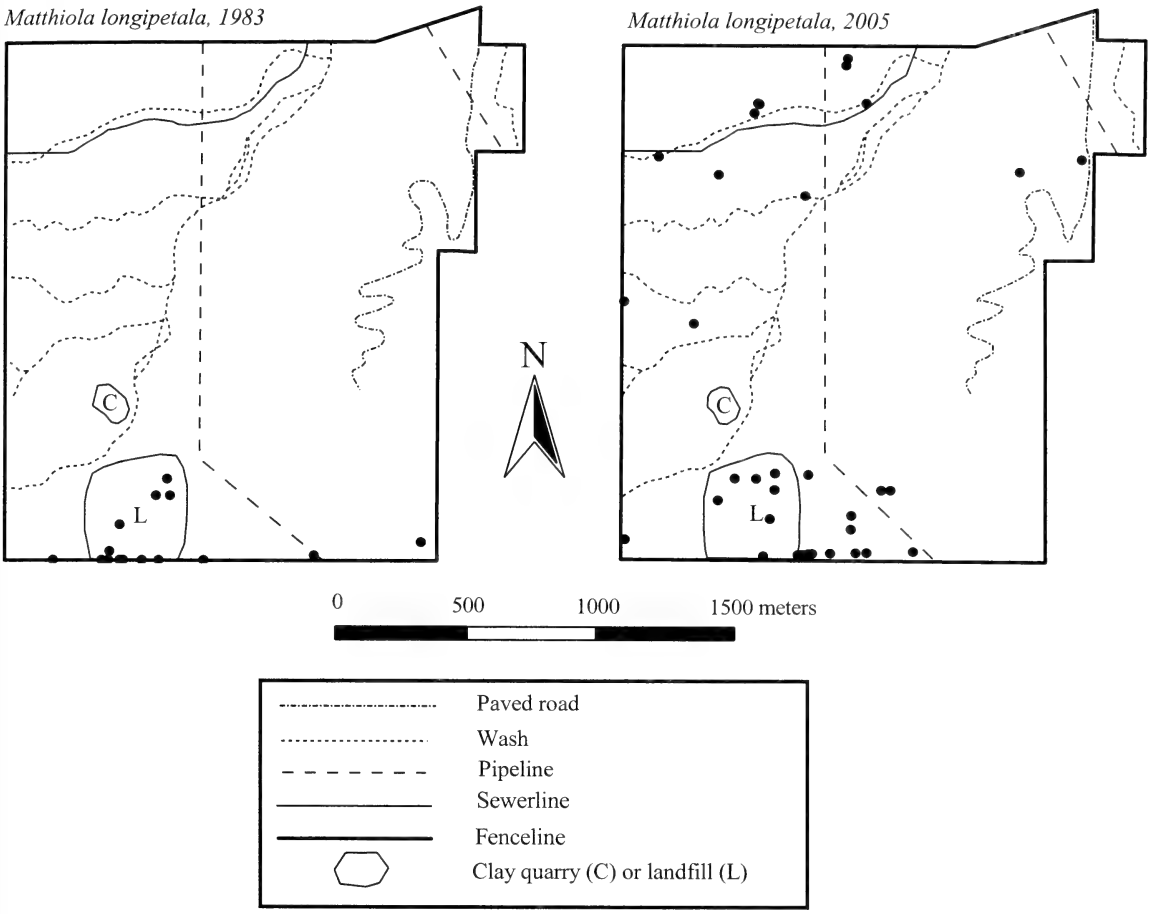

FIG. 3. Distribution of *Matthiola longipetala* at the Desert Laboratory, Tucson, Arizona, in 1983 and 2005.

murpheyi, Opuntia basilaris, O. santa-rita, Parkinsonia aculeata) are native to Arizona but not to the vicinity of Tucson (Kearney and Peebles 1969, Hodgson 2001). Seedlings of *A. murpheyi* were planted at the Desert Laboratory in 1987 as part of an archeological experiment (S. Fish, personal communication); some persisted without irrigation and eventually reproduced by offsets. The other three are cultivated as ornamentals near our study site. Two exotic species found during the surveys (*Lantana urticoides, O. engelmannii* var. *linguiformis*) are native to North America north of Mexico but not to Arizona (Correll and Johnston 1970). Both are grown near our study site as ornamentals. The remaining 46 species were introduced into North America north of Mexico, generally from the Old World or Latin America.

The exotic flora was dynamic during the 22 years between surveys. In 1983, we encountered 34 species of exotics along the gridlines. During the 2005 survey, we found 44 species. Eight species present in 1983 were not found in 2005 and probably no longer occur on our study site. Eighteen species found in 2005 were not encountered during the 1983 survey. Most were not known from the flora of the Desert Laboratory at the time and probably colonized the study site afterward.

Since 1983, there has been a major shift in the exotic flora from agricultural and ruderal weeds to ornamental plants, that is, species cultivated with or without irrigation in yards, gardens, and lawns. Specifically, ornamentals comprised 26% of exotic species in 1983 and 50% in 2005. In addition, overall frequency of ornamentals increased between 1983 and 2005 (Fig. 1). The growing need for water conservation in the southwestern United States has brought about increased use of arid-adapted ornamentals in urban and suburban landscaping (Mack 2002). Once introduced, ornamentals that are adapted to arid climates elsewhere can spread rapidly in the Sonoran Desert because they tolerate low rainfall, full sunlight, and unenriched soils (Mack 2002). As a consequence, desert areas near towns and cities support ever-increasing numbers of ornamentals. Ornamentals as a group have typically

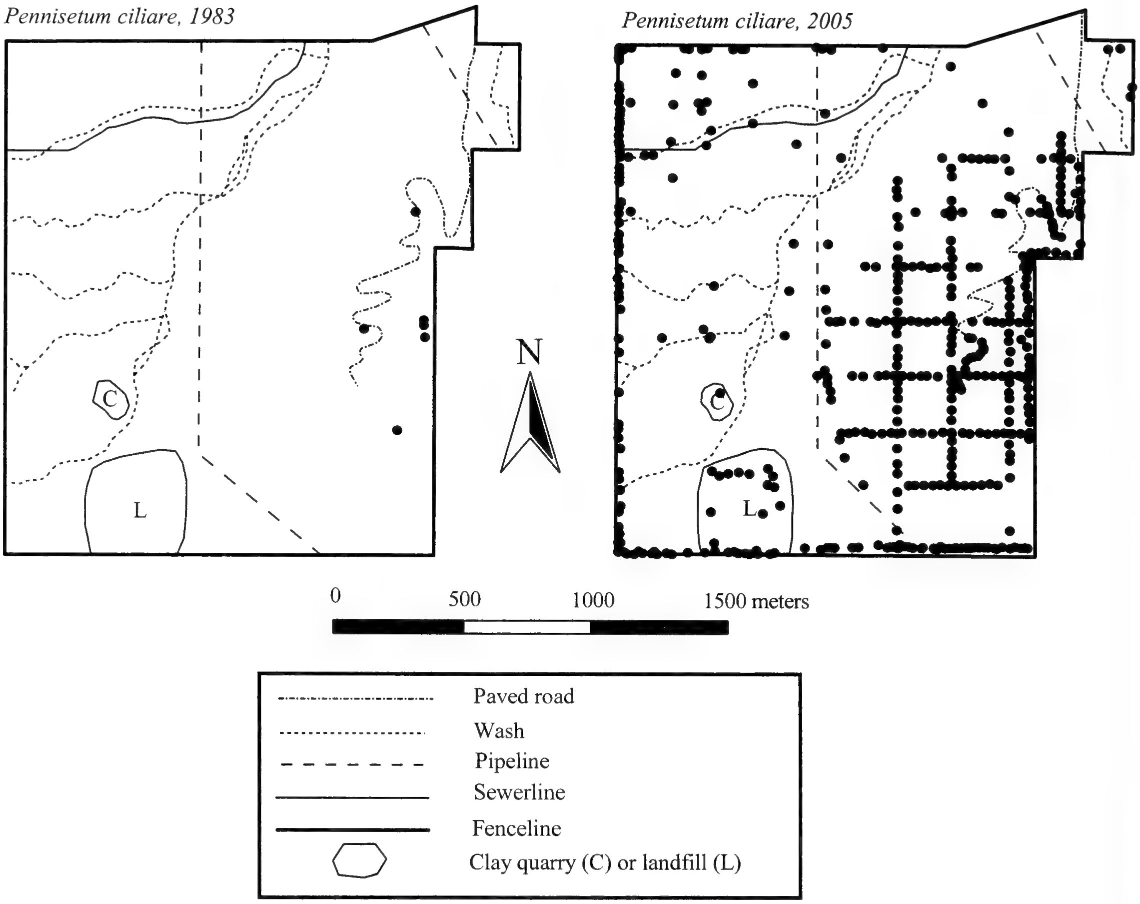

FIG. 4. Distribution of *Pennisetum ciliare* at the Desert Laboratory, Tucson, Arizona, in 1983 and 2005.

colonized the Desert Laboratory grounds from the perimeter inward, sometimes using washes as corridors (Fig. 1). Virtually all ornamentals on the study site in 2005 also could be found in nearby housing developments, a fact that emphasizes the vulnerability of urban natural areas to urban horticulture. Local and state governments need to take an active role in regulating the sale of invasive ornamental exotics in Arizona.

Status of Exotic Plants

Casual, naturalized, and invasive exotics comprised 44%, 40%, and 15% of species found during the two surveys. All exotics found in 1983 or 2005 are listed in Tables 1, 2, or 3. In 1983, mean frequency (number of coordinate locations) was 3.7 ± 4.40 for casual exotic species, 19.9 ± 18.55 for naturalized species, and 366.5 ± 253.06 for invasive species. (All means are ±1 SD) Categories differed significantly in mean frequency (Kruskal-Wallis test statistic = 19.15, $P < 0.001$). Means were also significantly different in 2005, when frequency averaged 2.5 ± 1.81 for casual species, 21.3 ± 17.42 for naturalized species, and 404.6 ± 339.94 for invasive species (Kruskal-Wallis test statistic = 29.01, $P < 0.001$). (Note that means excluded species with frequency = 0).

Casual exotic plants. After introduction to a site, casual exotic plants must surmount environmental and reproductive barriers before they can be considered naturalized (Richardson et al. 2000). Eight casual species disappeared from our study site between 1983 and 2005 (Table 1), presumably having failed to cross those barriers. Their populations were small in 1983 and therefore vulnerable to extirpation (reproductive barrier); in addition, annual precipitation at the study site in 2001, 2002, and 2004 was <70% of the long-term average, and severe drought stress might have killed many or most individuals, especially ornamentals that require supplemental water (local environmental barrier). Eleven casual species, all ornamentals, first appeared on our gridlines in 2005 (Table 1). More time is needed to determine whether any can maintain persistent populations.

Naturalized plants. Of 21 naturalized species encountered during the surveys (Table 2), the

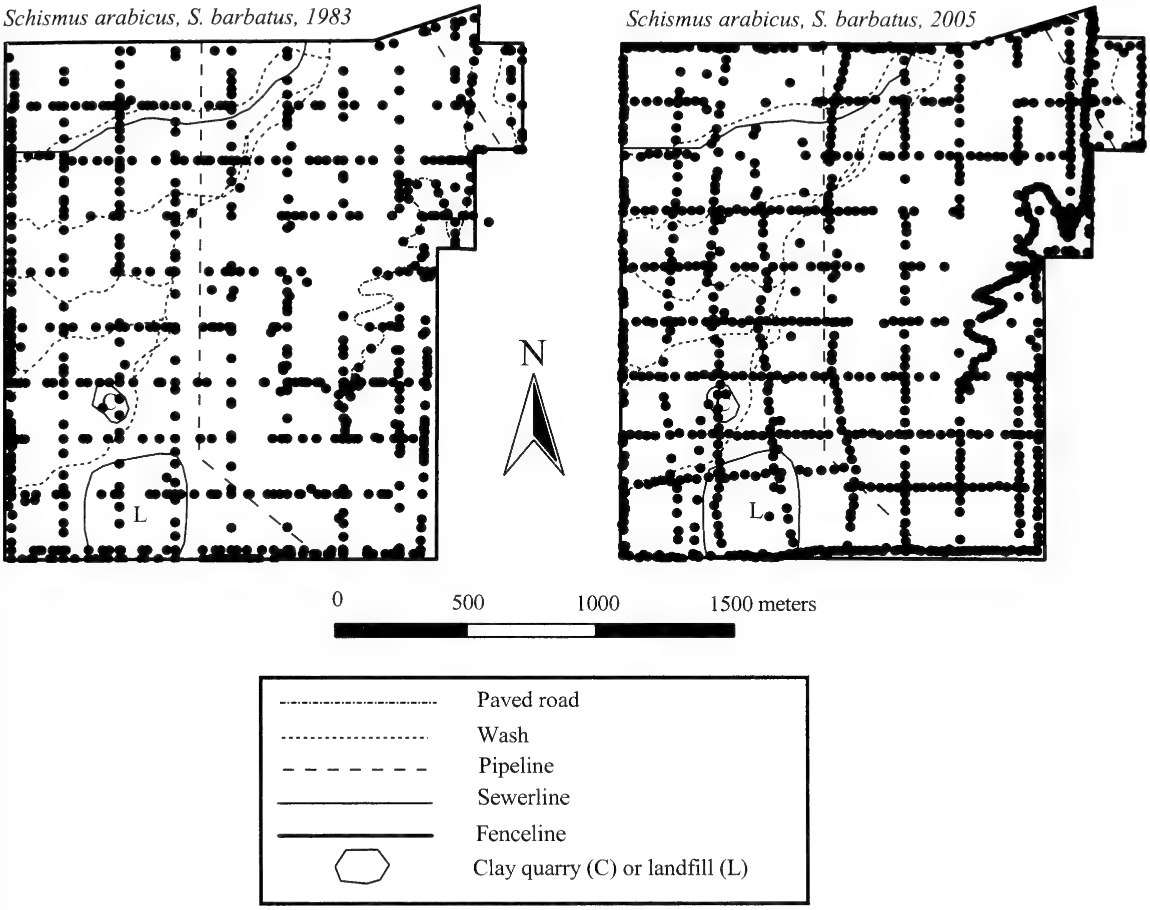

FIG. 5. Distribution of *Schismus arabicus* and *S. barbatus* at the Desert Laboratory, Tucson, Arizona, in 1983 and 2005.

mapped distribution of 11 expanded noticeably during the past two decades. Two are of particular concern because they have proven invasive elsewhere in the Sonoran Desert. Between 1983 and 2005, *Brassica tournefortii* spread from the perimeter of the study area into the interior and more than doubled in frequency (Table 2); in fact, its 2005 frequency was the highest of any naturalized exotic (Table 2). *Pennisetum setaceum*, not recorded in the 1983 survey, was present in 2005 at a higher frequency than average for naturalized plants (Fig. 2; Table 2). Neither *B. tournefortii* nor *P. setaceum* was ubiquitous and abundant on the Desert Laboratory grounds in 2005, but their invasive potential is well known (Wilson et al. 2002), and both require close monitoring. Although the other nine species are of less immediate concern, they still bear watching. *Bromus catharticus, Parkinsonia aculeata, Melilotus indicus*, and *Tamarix chinensis*, for example, were present at low frequency in 1983, but that frequency more than doubled by 2005 (Table 2). In 2005, frequency and percent change for *Matthiola longipetala* were still relatively low (Table 2), but the scatter of locations in 2005 was considerably wider than in 1983 (Fig. 3). The same was true of *Avena fatua. Eragrostis echinochloidea, Opuntia engelmannii* var. *linguiformis*, and *Rhus lancea* apparently colonized the study site after 1983; by 2005 these species were scattered widely enough to be considered naturalized. Frequency of the remaining naturalized species either decreased or stayed the same between surveys (Table 2).

Invasive plants. Invasive species at the Desert Laboratory included seven annual forbs and grasses and one perennial grass (Table 3). Two of these species have become invasive since the original survey. *Herniaria hirsuta* subsp. *cinerea* was rare and local when first reported from the Desert Laboratory (Bowers and Turner 1985) but in 2005 was widespread (Fig. 2). Although its frequency was low relative to long-established invasives such as *B. rubens* and *E. cicutarium* (Table 3), we are treating *Herniaria* as invasive because it has spread widely from its original

FIG. 6. Distribution of *Sisymbrium irio* at the Desert Laboratory, Tucson, Arizona, in 1983 and 2005.

location, it has colonized undisturbed as well as disturbed habitats, and it is often abundant where found. In 2005, *Pennisetum ciliare* was declared a regulated and restricted noxious weed in Arizona. Between 1983 and 2005, frequency of this species on our study site changed by almost 8000%, by far the largest increase for any species (Fig. 4; Table 3). During those 22 years, plants spread from "isolated pockets" (Burgess et al. 1991) to form several continuous stands, the largest of which occupied about 50 ha in 2004. This species is abundant not only on disturbed sites such as the landfill and roadsides, but also on undisturbed rocky slopes (Fig. 4). It tends to become the dominant species wherever it occurs.

In contrast to the dramatic spread of *H. hirsuta* and *P. ciliare*, increases in *Schismus* and *Sisymbrium irio* were relatively modest (Table 3). Although the increase in *Schismus* could conceivably reflect differences in sampling methods, careful comparison of the distribution maps shows that this species evidently colonized additional territory between 1983 and 2005, for example, along the paved road and the northern boundary (Fig. 5). *Schismus barbatus* often germinates in years that are too dry for native winter annuals (Venable and Pake 1999), which likely facilitates spread (Burgess et al. 1991). Another facilitating factor is that *Schismus* seeds are persistent, lasting in the soil for at least two years (Pake and Venable 1996). Even after dry winters when few seeds germinate, a large reserve of seed remains, enabling populations to rebound given adequate rain in the following winter (Venable and Pake 1999). Seeds of *Sisymbrium irio* are also persistent (Pake and Venable 1996). As for *Schismus*, the buffering effect of a between-year seed bank might explain why its frequency and distribution (Fig. 6; Table 3) did not decline during recent dry winters.

Three invasive species—*B. rubens, Hordeum murinum*, and *E. cicutarium*—declined between 1983 and 2005 (Table 3). These declines do not indicate a reversal of status from invasive to naturalized but, rather, likely reflect the combined effects of seed-bank dynamics and climatic variability. Seeds of *B. rubens*, for example, are transient in the soil, lasting no more than one

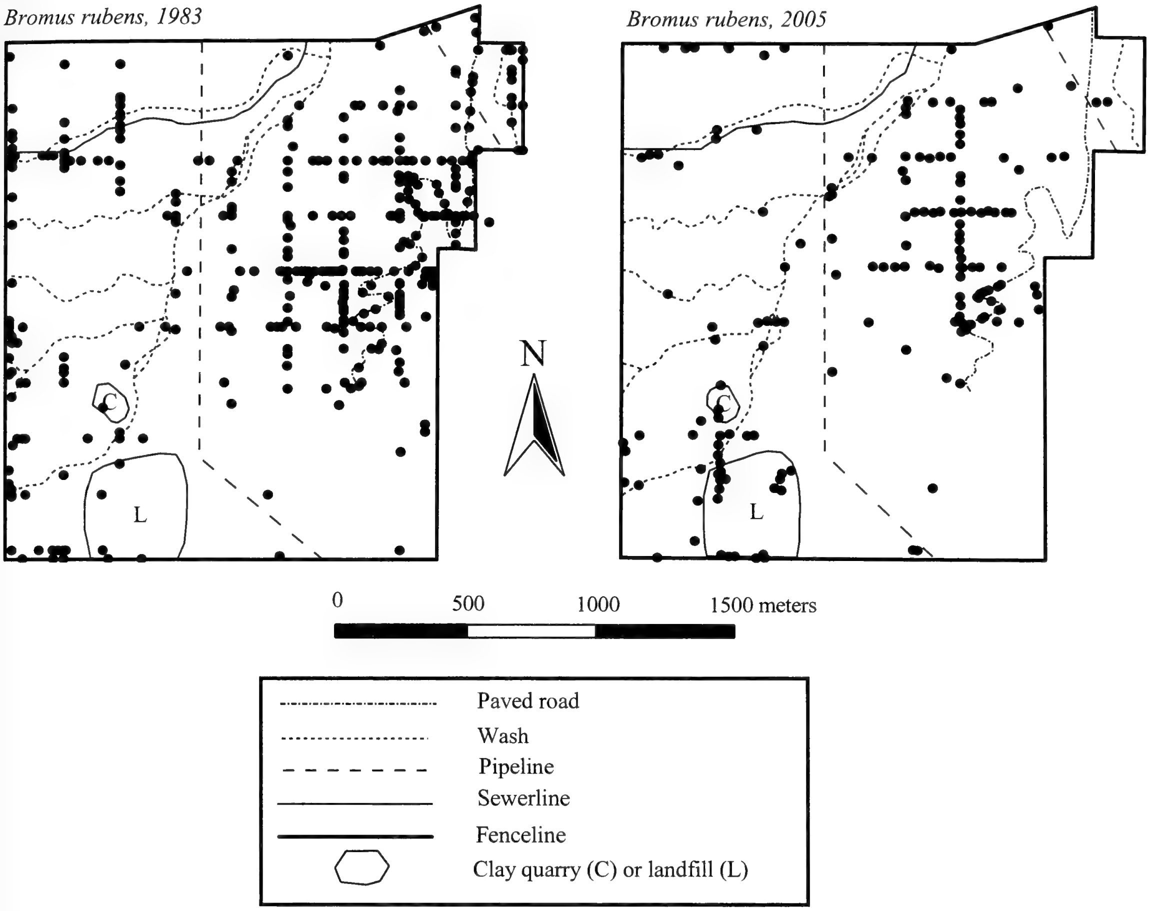

FIG. 7. Distribution of *Bromus rubens* at the Desert Laboratory, Tucson, Arizona, in 1983 and 2005.

year (Pake and Venable 1996; Salo 2005). During recent dry winters, seeds germinated only in moist microsites, leading to small populations, lowered seed production, and, eventually, decreased frequency in 2005 compared with 1983 (Fig. 7; Table 3). A similar mechanism could account for the decline in *H. murinum*, seeds of which are not likely to persist in the soil between years (Popay 1981). *Erodium cicutarium* was only slightly less frequent in 2005 than in 1983 (Table 3). This species maintains large between-year seed banks in some locations (Roberts 1986; Mayor et al. 1999) but perhaps not at our study site (Pake and Venable 1996). The fact that *E. cicutarium* declined less dramatically than *B. rubens* or *H. murinum* suggests that there is a small reserve of persistent seeds in the soil. Other possible explanations for the decline of *B. rubens, H. murinum*, and *E. cicutarium* include competition with *P. ciliare*, especially in dense stands on rocky slopes, competition with native winter annuals, and lower germination as a result of the drier winter (151 mm in 2005 versus 250 mm in 1983).

Residence Time and Status of Exotics

In Chile and doubtless elsewhere, geographical extent of exotic species has increased with time since introduction (Castro et al. 2005). At the Desert Laboratory, casual, naturalized, and invasive exotics differed in minimum residence time, with casual species having been present for the shortest time and invasive species for the longest. Specifically, residence time for casual, naturalized, and invasive species averaged 14.5 ± 10.96 years, 28.1 ± 18.17 years, and 52.3 ± 32.51 years; the difference among categories was significant (Kruskal-Wallis test statistic = 16.146, $P < 0.001$). Moreover, as noted above, frequency in 1983 and 2005 increased across categories from casual to naturalized to invasive. These trends suggest that the longer a species was present on our study site, the more likely it was to surmount barriers to naturalization and invasion. The recent surge in ornamental exotics, combined with temporal trends in invasiveness, indicates that the proportion of invasive species in the flora will increase over time.

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CONSERVATION OF PERIPHERAL PLANT POPULATIONS IN CALIFORNIA

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ABSTRACT

The conservation of peripheral plant populations is paradoxical. Populations occurring on the edge of a species' range tend to be smaller, more isolated, and more genetically and ecologically divergent than central populations. The combination of these characteristics can impart novel evolutionary potential and local ecological significance, thus heightening their conservation value, while also making them less viable and more prone to local extinction. Public policy supports the conservation of peripheral populations, despite the commonness of the species elsewhere. However, the conservation of significant peripheral populations of nonlisted plants has been arbitrary and ineffective. The absence of explicit criteria to determine the conservation value of peripheral plant populations, the lack of finer-scale data on plant distributions, and a general unawareness of their value have hindered efforts to conserve them. We review the conservation value of peripheral plant populations and, using California as an example, describe regulatory methods to improve their conservation. We also propose a scheme to assess a population's conservation value.

Key Words: California flora, CEQA, HCP, local rarity, NCCP, peripheral populations, rare plants.

Peripheral populations occur on the geographic edge of a species' range. Depending on the scale used to define them, peripheral populations can be completely isolated from conspecifics, and therefore considered disjunct, or can occur in closer proximity to other marginal populations. While the evolutionary significance of peripheral populations has long been recognized, other than for rare, threatened, or endangered species, their conservation value typically receives little attention.

In this paper, we review the conservation value of peripheral plant populations. Using California as an example, we highlight how regulatory policy can and should be utilized to conserve biologically and culturally significant peripheral populations of otherwise-common species. We also propose a scheme to assess the potential conservation value of peripheral populations.

Due to their geographically marginal location, peripheral populations tend to exhibit lower and more-variable densities and are more fragmented than central populations in a species' range (Fig. 1) (Mayr 1970; Lawton 1993; Channell and Lomolino 2000; Gaston 2003). For plants, peripheral populations are more likely to be influenced by different selective factors than central populations, including climate and soils, plant community assemblages, and disturbance regimes (e.g., fire intensity and interval). Ecologically distinct peripheral populations also can occur when geographically marginal populations occupy suboptimal or different habitats than more-central conspecifics (Soule 1973; Hoffmann and Blows 1994; Lesica and Allendorf 1995). Morphological or ecological divergence in peripheral populations resulting from differing geographic selection regimes is one form of clinal variation and can be a precursor to speciation (Mayr 1970; Garcia-Ramos and Kirkpatrick 1997). Due to the greater influence of population bottlenecks, founder effect, and genetic drift, peripheral populations can be genetically distinct from central populations. These differences in genetic structure can result in distinct genotypes and phenotypes and impart enhanced evolutionary potential for adaptation and speciation (Levin 1993; Garcia-Ramos and Kirkpatrick 1997; Lammi et al. 1999). Thus, the combination of geographic isolation and genetic divergence driven by directional selection can give peripheral populations novel evolutionary trajectories, in comparison to central populations (Lesica and Allendorf 1995; Nielsen et al. 2001; Gaston 2003). The isolation and decreased population size or abundance of peripheral populations, for instance, strongly favors the evolution of self-compatible breeding systems in otherwise self-incompatible species (Busch 2005).

Small, isolated populations, as often occur on the periphery of a species' range, also tend to have lower levels of heterozygosity and allelic variation than larger, more-central populations (Lesica and Allendorf 1992, 1995; Lawton 1993;

In comparison to core populations, peripheral populations tend to:

- be smaller,
- have more-variable densities,
- be ecologically distinctive,
- occur in marginal habitats,
- experience different selective regimes,
- have restricted gene flow,
- undergo greater rates of genetic drift,
- have less genetic variation,
- have increased population-level differentiation,
- have greater extirpation risk, and
- be morphologically similar

FIG. 1. Peripheral populations compared to core populations.

Lammi et al. 1999; Busch 2005) and thus may have decreased fitness and an increased risk of extirpation (Gaston 2003; Reed 2004). For this reason, the conservation of peripheral populations is controversial, because they tend to be less stable and are viewed by some as sink populations likely to be extirpated anyway, despite conservation efforts (Peterson 2001). By this rationale, the inclusion on state and federal endangered species lists of peripheral populations of species that are otherwise common and demonstrable secure elsewhere dilutes limited conservation resources that could be better focused on species with narrowly-restricted distributions or species of greater risk throughout their range (Peterson 2001).

However, the genetic diversity and structure and viability of a population is determined by many factors, including its degree of isolation and spatial pattern, gene flow, varying directional selection, and the species' reproductive strategies. Therefore, a population's viability can depend more on demographic structure and population dynamics (Bevill and Louda 1999) (e.g., whether the species is formerly common or historically rare [Brigham 2003]) than on its genetic structure. As well, lower levels of genetic diversity are not always associated with lower levels of fitness. For example, in a comparative study of central and peripheral populations of a rare European herb, *Lychnis viscaria* L. (Caryophyllaceae), Lammi et al. (1999) found that while genetic diversity was positively correlated with population size, no correlation was found between lower genetic diversity of peripheral populations and measured fitness characters such as seed set, seed germination, and seedling mass.

Contrary to Peterson (2001), under certain circumstances, geographic isolation actually predisposes peripheral populations to a greater survivorship than larger, more-central populations. In analyzing range contractions of 245 plant and animal species, Channell and Lomolino (2000) found that when species undergo catastrophic range contractions (>75%), populations on the edge of the range have significantly greater survivorship than core populations. This enhanced survivorship is the result of localized extinction events being primarily both anthropogenic and spatially autocorrelated. In other words, populations that persist the longest and act as refugia for a species tend to be those least (or last) affected by the spread of extinction forces (Channell and Lomolino 2000).

Thus, the conservation value of peripheral populations is paradoxical. On the one hand, peripheral populations can have enhanced ecological and evolutionary significance. On the other hand, this significance can be both a cause and a consequence of their isolation and small size and therefore correlated with reduced viability and increased extinction risk. While expert opinion is not unanimous about the conservation value of peripheral populations, the biological and intrinsic values of these populations are well documented and summarized as follows:

1) Their high potential for genetic distinctiveness and divergence can impart novel evolutionary pathways for future migration and speciation events (Levin 1993; Noss 1994; Lesica and Allendorf 1995; Garcia-Ramos and Kirkpatrick 1997; Nielsen et al. 2001; Gaston 2003).
2) The maintenance of genetic variation in the form of small, isolated populations contributes to long-term species survival and preservation of local genetic diversity (Millar and Libby 1991; Lesica and Allendorf 1992; Fiedler 1995; Lesica and Allendorf 1995; Lammi et al. 1999; Channell and Lomolino 2000; Caballos and Ehrlich 2002; Gapare and Aitken 2005; Gapare et al. 2005).
3) Even very widespread taxa (e.g., bison, sea otter, passenger pigeon, American elm, American chestnut) have been regionally extirpated or brought to the brink of extinction in a short time span (Nielsen et al. 2001).
4) Peripheral populations can have important local human values, (e.g., cultural, economic, and historical) regardless of how common the species may be elsewhere (Hunter and Hutchinson 1994; Gaston 2003).

Despite their conservation value, there are, at present, no explicit criteria to determine the conservation priority of peripheral populations. Lesica and Allendorf (1995) provide a useful theoretical framework for evaluating a population's conservation value that emphasizes the combination of geographic isolation and ecological distinctiveness as principal criteria. We agree that the degree of spatial isolation and ecological distinctiveness are the best criteria for assessing a population's conservation significance, especially in the absence of population genetics data. However, without some means to quantify or otherwise characterize spatial isolation or ecological distinctiveness, the conservation of these populations cannot be substantially improved during regional planning or the review of projects that may affect them. Furthermore, with the notable exception of Millar and Libby (1991), we find little guidance for conservation biologists on strategies to protect significant populations of widespread plants.

In this paper, we focus our discussion of conservation and land use planning strategies on California for the following reasons. First, California occupies a central biogeographic location and zone of ecological transition on the Pacific Coast of North America, so its floristic diversity includes many widespread taxa on the edge of their range. Second, California has the largest state flora in the nation and extraordinary topographic, geologic, and climatic habitat heterogeneity. Third, California has some of the strongest environmental regulations in the hemisphere, e.g., the California Environmental Quality Act (California Environmental Quality Act 2005) (CEQA), and the California Endangered Species Act; see Morey and Ikeda (2001) for an overview of state and federal laws and regulatory programs used to conserve California plants. Fourth, many of California's ecosystems and plant communities are highly threatened (Hobbs and Mooney 1998). California, for example, has a higher percentage of wetlands loss (an estimated 91 percent loss between the 1780's and 1980's) than any other state (Dahl 1990).

Reasons why Public Policy has been Arbitrary and Ineffective

Political Boundaries: a Conservation Tool and Impediment

Political boundaries, although not always arbitrary in their location, generally do not correspond with significant range boundaries for organisms. Interestingly, this lack of correspondence is less pronounced in the Old World, where political dynamics have more often coincided with constraints imposed by local terrain. In the New World, political boundaries were drawn after the onset of the Age of Reason and are more likely Cartesian or the results of formulistic procedures. As a result, political boundaries as a rule do not correspond with landscape discontinuities, with floristic provinces and districts, or with the conservation relevance of a population (Rodrigues and Gaston 2002).

Toward the periphery of many species' ranges, some populations are found to a lesser extent in the next political unit and are thus rare in that unit (Abbitt et al. 2000; Gaston 2003). A good example is *Sequoia sempervirens* (D. Don) Endl. (coast redwood) (Taxodiaceae), primarily a California species whose range extends into the state of Oregon, where it is rare. Other species exhibit the same pattern because the California Floristic Province extends into southwestern Oregon.

Because conservation efforts, both public and private, are primarily organized and managed within political units, conservation classification schemes routinely take differing geographic units into account in order to capture regional rarity as well as global rarity. Examples include the California Native Plant Society's (CNPS) Inventory of Rare and Endangered Plants, which includes List 2 (plants rare, threatened, or endangered in California, but more common elsewhere) and a RED code combination (i.e., rarity, endangerment, and distribution) that includes D = 1 (distribution is more or less widespread outside of California) (California Native Plant Society 2001). State heritage programs with ranks such as G5S1 (globally common and widespread, extremely rare and restricted in California) portray a similar geographic distribution (California Natural Diversity Database 2005). In these cases, the range of taxa extends into California to a sufficiently small degree that they are considered rare here.

Conservationists have typically accorded less concern to taxa in these circumstances than they have given to globally rare species. We agree with this general approach. Nevertheless, we contend that it is precisely those "state rare but globally widespread" species that provide the opportunity to reexamine peripheral populations for their conservation significance. Furthermore, a G5S1 RED code status illustrates an important consideration regarding the conservation of populations in these circumstances—namely, that they may warrant heightened conservation status, not because they happen to fall within a political boundary that makes them rare, but rather because they are much more likely to be peripheral populations having the attributes described earlier (Abbitt et al. 2000). Thus, conservationists seeking to preserve the unique and rare plants within their political boundaries also may be helping to conserve widespread species by focusing on their peripheral populations (see Hunter and Hutchinson 1994).

Conservation of Taxonomic Units Emphasizes Morphological Distinctiveness

Among the many important traits that allow plants to persist, morphological variation is crucial and is recognized for its importance. Coarse-level morphological variation is the preferred class of attributes used for plant identification and, before the advent of formal taxonomy, served as the basis for the so-called folk taxonomies. Moreover, morphological variation, in circumscribable and repeated patterns of distinctiveness, continues to be the primary basis for distinguishing among formal taxonomic units. In other words, variation among populations that results in morphological distinctness is more likely to lead to unique taxonomic status (Panchen 1992). Given that taxa (both species and subspecific taxa) are the principal units that are accorded conservation priority (when certain criteria are met), we argue that important classes of biologically significant variation are routinely overlooked as a basis for conservation efforts.

The significance of this issue is illustrated in the hypothetical examples shown in Figure 2. For these two scenarios, we consider the identical geographical distributions of populations: one large core range of populations in proximity to each other with an overall widespread geographic extent, and one small range of peripheral populations. In this case, the populations are also disjunct and largely isolated from the core. Under scenario A, disjunct populations are morphologically similar to the core populations, and thus given equal taxonomic status, called Taxon 1. In scenario B, while the populations also are closely related, the disjunct populations have distinctive morphological variation that leads to a unique taxonomic status, one for the core populations, Taxon 2, and one for the peripheral populations, Taxon 3. Thus, they are also sister species. These two scenarios portray the differing taxonomic results for two otherwise-equal geographic distributions of populations. What if the disjunct populations in scenario A (Taxon 1) have unique substrate or temperature tolerances? What if their underlying genomic variation is substantially different from the core population? What if they produce unique secondary compounds that afford them herbivore or disease resistance? All of these are possible and, indeed, are more likely in peripheral populations. Yet, they would not receive conservation status under scenario A, while they would under scenario B.

Assessing Conservation Criteria, Values, and Priorities

Although theoretical rationales for conserving peripheral populations are well developed, practical methods for evaluating their conservation value are compromised by the difficulty of collecting data, or by the fact that existing data are not organized specifically for this purpose. Nevertheless, a number of authors have proposed useful criteria for assessing the conservation value of peripheral or other special plant populations; these include isolation and distance, as well as genetic, environmental, evolutionary, life history, threat, and utilitarian attributes (Millar and Libby 1991; Holsinger 1992; Hunter and Hutchinson 1994; Schemske et al. 1994; Lesica and Allendorf 1995; Nielson et al. 2001).

Many of these categories overlap or are highly correlated. For example, environmentally distinctive populations are likely to be genetically distinctive, and thus may have greater evolutionary potential, depending on a number of other circumstances. Also, distantly isolated populations are more likely to be genetically distinctive, or occupy habitats that differ from core populations. As satisfying as these categories are biologically, they are not equal in terms of setting and implementing criteria for conservation.

Assessment of genetic distinctiveness should be a primary means for identifying peripheral populations of high conservation value. Indeed, because of the number of population genetic studies of plant populations, we have learned that significant levels of genetic variation often do not correlate with the features used for taxonomic demarcation. Genetic variation among populations is important because it is the basis for both environmental distinctiveness and evolutionary change. We agree that studies of these kinds should be conducted whenever possible. Unfortunately, genetic data are expensive and time consuming to retrieve and are not available for most California plant populations, with the exception perhaps of commercially important conifer species. Given the rate at which plant habitat is being lost and peripheral populations are disappearing, a practicable approach is needed to evaluate the conservation value of a given population.

Here, we propose three categories of criteria for evaluating the conservation significance of a peripheral population: 1) geographic isolation, 2) environmental distinctiveness, and 3) intrinsic human values. The first two criteria derive from Lesica and Allendorf (1995), who emphasize the importance of genetic drift and intensity of selection. The third criterion derives from many sources, but is well articulated by Hunter and Hutchinson (1994). These three attributes are the easiest to assess among all the criteria discussed above. Those populations that meet one or a combination of these criteria should be accorded a greater conservation value. Those that are also threatened or endangered should be given even greater value.

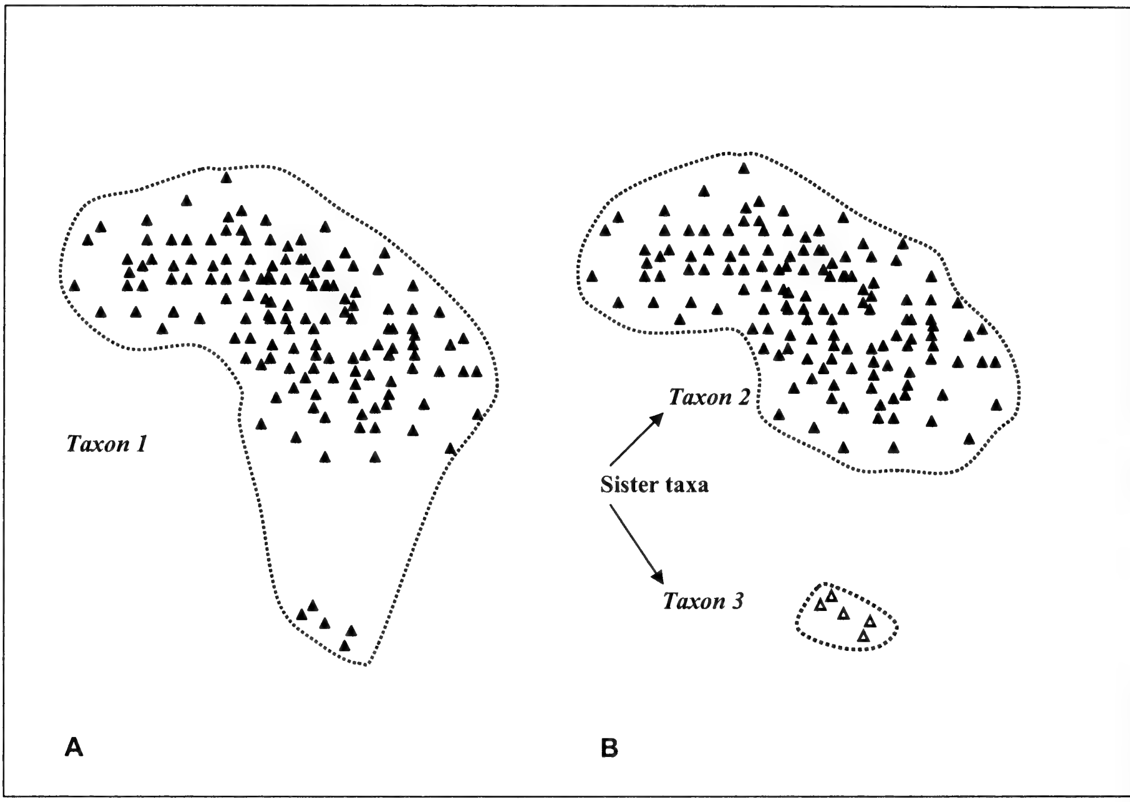

FIG. 2. Geographical distributions of two hypothetical scenarios that include a peripheral population. A) The peripheral populations are taxonomically part of *Taxon 1*. B) The peripheral populations, *Taxon 3*, are the sister species, or a closely related congener, to *Taxon 2*, the core population.

Geographic isolation criterion. Populations that are distant from core populations are, by definition, more likely to be on the periphery and thus be considered peripheral or, in some cases, disjunct populations. Also, the greater the distance from core populations, the more likely peripheral populations are to be genetically isolated and have distinctive traits with evolutionary importance. This criterion thus formalizes focusing on peripheral populations and has a significant biological rationale for inclusion.

This criterion should reflect distances that correspond to an evolutionarily significant degree of genetic isolation between peripheral and core populations. In some cases, nearest neighbor population distances will provide suitable comparative distances. However, consideration should be given to the overall geographic structure of the species' range and the specific methods used to characterize them (Gaston 2003; White 2004). The application of this criterion should also take into account life history attributes (e.g., mode of pollination, seed dispersal, life span). Because life histories vary greatly, no standard measure of geographic isolation can be utilized to assess the conservation significance of populations among diverse taxa.

Environmental distinctiveness criterion. Populations that occupy unusual or unique habitats are likely to have unique genetic traits, when compared to populations occupying core areas of the range (e.g., peripheral populations associated with community types, vegetation stands, or habitats that differ significantly from core populations). Populations in environmentally distinct locations are also more likely to have evolutionary significance. Thus, we consider environmental distinctiveness another critical category.

To more explicitly assess both environmental distinctiveness—and, to some degree, the functional spatial isolation of a peripheral population—we propose using the geographic subdivisions of Hickman (1993). Hickman utilizes a nested, four-tiered system of provinces, regions, subregions, and districts to divide California into meaningful biogeographic units. These subdivisions are, to the greatest extent possible, based on three main biologically relevant criteria: topography, climate, and vegetation type (Hickman 1993). For example, if a population is unique to a given subdivision or is isolated from conspecifics by one or more differing subdivisions, then this population would have, by definition, greater environmental and geographic distinctiveness

and isolation than would a peripheral population occurring in the same subdivision as the rest of its distribution. This approach benefits from being easily replicated outside of California by utilizing similar biogeographic subdivisions (e.g., those of Cronquist et al. 1972; Takhtajan 1986; Ricketts et al. 1999; Oregon Natural Heritage Program 2001).

Intrinsic human values criterion. Finally, conservation biology is highly value laden. The many, often idiosyncratic, and sometimes competing human values, ethics, and predilections play an important role in the conservation decision-making process (Noss 1994). There is general agreement that a population's cultural, economic, historic, and even aesthetic value enhances its conservation value. Local humans often assign important intrinsic values to local species, if for no other reason than they like having them on their landscape. Leopold (1949) captured this sentiment well: "Relegating grizzlies to Alaska is about like relegating happiness to heaven; one may never get there." Therefore, all things being equal, peripheral populations that have important human values would have greater conservation value than those that do not (see also Holsinger 1992). It is important to note that societal values change through time and that through education and effective public relations, the conservation community affects this change.

Examples of Populations that Merit Conservation

Here, we give three examples of taxa (Sitka spruce, lodgepole pine, and various orchid species) with relatively widespread California distributions possessing regionally significant populations with conservation value. Nomenclature follows Hickman (1993).

Picea sitchensis (Bong.) Carr. (Sitka spruce) (Pinaceae) is a Pacific Northwest coastal conifer and economically important timber tree, occurring from Alaska to northern California. Sitka spruce has a continuous distribution that terminates just south of Humboldt Bay in Humboldt County; however, a disjunct population occurs near Fort Bragg, Mendocino County, approximately 100 km to the south (Smith and Wheeler 1992; Lanner 1999).

In a comparative study of the genetic diversity of Sitka spruce throughout its range, Gapare et al. (2005) determined that peripheral and core populations have similar measures of heterozygosity; however, the only allele they classified as rare and localized was limited to disjunct and peripheral populations, including the Fort Bragg population. Gapare et al. (2005) demonstrate that peripheral and disjunct populations of this species have value for *in situ* conservation of rare alleles. In a related analysis, Gapare and Aitken (2005) found strong spatial genetic structure in peripheral populations, but not in core populations. This striking difference in the distribution of genetic variation among Sitka spruce population classes has important implications for size and location of *in situ* reserves and sampling strategies for *ex situ* conservation and research collections (Gapare and Aitken 2005).

Thus, this disjunct Fort Bragg Sitka spruce population has regional ecological, evolutionary, and economic significance because of its rare genetic geographic variation and dominance in local forest community structure.

Pinus contorta Dougl. ex Loud. (lodgepole pine) (Pinaceae) is a conifer widely distributed from the Yukon south to California and the Rocky Mountains, with a disjunct population in Baja California. It is extremely ecologically variable, with four named geographic subspecies (Critchfield 1957, 1980). It is a dominant tree species in many montane and coastal regions of western North America, and as such, is important both ecologically and economically. All four subspecies of lodgepole pine are represented in California, with northern California having much higher levels of heterozygosity and allelic diversity, compared to more northern and Rocky Mountain populations (Oliphant 1992).

In the Klamath Region of northern California, an undescribed lodgepole pine race, or ecotype, occurs on ultramafic substrates (serpentine soils). This race is referred to by Griffin and Critchfield (1972) as "an unnamed closed-cone race in the low mountains of Del Norte County" and by Critchfield (1980) as the "Del Norte race." Oliphant (1992) found that Del Norte race populations have low levels of expected heterozygosity and possess a suite of rare alleles; however, none are unique to the race. Kruckeberg (1967) demonstrated a differential growth response, with plants from non-ultramafic soils growing slower than plants from ultramafic soils when grown on an ultramafic substrate. Populations of the Del Norte race probably represent a distinct serpentine ecotype (Oliphant 1992). Though lodgepole pine is a common species in California and western North America, these Del Norte race populations occupy edaphically extreme sites and represent environmentally peripheral occurrences with unusual genotypes.

Coleman (1995) presents the county-wide and regional distribution and conservation implications of California's native orchid flora (Orchidaceae). Although many of California's orchid species are widely distributed, Coleman elucidates why marginal populations in southern California and the Santa Cruz Mountains are sufficiently isolated and threatened to warrant conservation efforts. These taxa all have geographic ranges that extend at least as far north as Washington.

According to Coleman (1995), orchid populations on the edge of their range in southern California are threatened for the following reasons: 1) populations are extremely rare in San Bernardino and San Diego Counties and large populations in San Luis Obispo and Santa Cruz Counties have been lost to urbanization (*Spiranthes romanzoffiana* Cham.); 2) recent attempts to locate southern California populations have been unsuccessful (*Spiranthes porrifolia* Lindley); 3) populations are so few and tiny that the species could be eliminated from an entire county by a single stochastic event or timber harvest (*Piperia leptopetala* Rydb.); and 4) species apparently have been extirpated from the Santa Cruz Mountains by habitat destruction (*Cypripedium fasciculatum* S. Watson and *C. montanum* Lindley).

Unlike the two previous examples, we have no data that indicates these orchid populations are genetically or environmentally distinct. Orchids are however one of the most charismatic components of the California flora and are revered by lay naturalists and biologists alike for their beauty and unusual reproductive biology. For example, southern and central California alone has over six orchid societies, and their importance in the horticultural trade is manifest. Therefore, we contend that given the intrinsic value placed upon these species, their regional rarity, and documented habitat loss and range contractions, these scarce southern California and Santa Cruz Mountains orchid populations warrant protection during regional conservation planning efforts and review of projects potentially impacting or eliminating them.

Regulatory Process

California Environmental Quality Act

Here we review certain regulatory programs that could be more effectively used to conserve significant peripheral plant populations. In doing so, we aim to better integrate current understandings about the biological attributes of peripheral and disjunct populations with the broader aims of the California regulatory framework.

CEQA, together with the California and federal Endangered Species Acts (CESA and FESA, respectively), is a principal tool used to conserve rare and endangered species in California. CEQA is landmark legislation that requires (with some exceptions) that potentially significant environmental impacts resulting from a proposed project (e.g., a housing development, dam installation, or timber harvesting plan) be disclosed to the public and reviewing state agencies. Furthermore, CEQA (section 21002) states that (again, with exceptions) public agencies should not approve projects that do not include feasible alternatives or mitigations that will avoid or substantially lessen significant effects, when such feasible alternatives or mitigations exist (California Environmental Quality Act 2005). Article 9 of CEQA, Contents of Environmental Impact Reports [section 15125 (c)], states "Knowledge of the regional setting is critical to the assessment of environmental impacts. Special emphasis should be placed on environmental resources that are rare or unique to that region and would be affected by the project."

CEQA is of fundamental importance to plant conservation, because it addresses potential impacts to any species that can be shown to meet the criteria for state or federal listing (section 15380[d]) (California Environmental Quality Act 2005), as well as to CESA and FESA listed species. Yet, to our knowledge, CEQA rarely has been utilized to protect peripheral or otherwise locally significant populations of widespread plant species if the species could not be considered endangered, rare, or threatened pursuant to CEQA (section 15380[d]). Despite this, a fair argument can be made by public agencies and conservationists that potentially significant impacts to these populations must be disclosed and avoided if: 1) the population is locally rare or unique (pursuant to CEQA section 15125 [c]) and therefore may have intraspecific variation and potential evolutionary significance; 2) the population has regionally significant ecological importance; and 3) the population has local cultural, economic, or historic value.

Regional Conservation Planning

In California, land use planning on nonfederal lands is done on the local scale—most commonly through municipal and county general plans. However, regional planning also occurs under the auspices of state Natural Community Conservation Plans (NCCPs) Natural Community Conservation Planning Act (2002) and federal Habitat Conservation Plans (HCPs). NCCPs and HCPs in California are regional conservation planning tools used to protect habitats of CESA and FESA listed and potentially listed species across a large area. A principal objective of NCCPs is to bring about species recovery by protecting natural communities on which the species depends. The principal federal objective of an HCP is to minimize and mitigate impacts to listed species to the maximum extent practicable. Land owners often enter into HCPs because it is the only means to receive an incidental take permit for a federally listed species. An incidental take permit is a permit to incidentally "take" (kill) a listed species during the course of an otherwise-legal activity.

NCCPs and HCPs both hold greater promise in conserving listed species and significant por-

tions of their habitat, or even entire ecosystems, than project-by-project mitigations (Noss et al. 1997; Rolfe 2001; Hopkins 2004). Regional conservation plans are also potentially much more effective in protecting habitats and species from large-scale, spatially autocorrelated threats such as urbanization, climate change, sea-level rise, and invasive species, most of which typically are not addressed or mitigated for effectively by smaller projects outside the HCP/NCCP realm. Regional conservation planning is potentially more effective in addressing cumulative impacts than are multiple, smaller-scale projects subjected to CEQA individually (Noss et al. 1997; Hopkins 2004). This is because cumulative impacts assessment is essentially a large-scale and rate-determined process not well suited to smaller, multiple, ongoing, regionally concentrated projects such as timber harvesting plans in a watershed or urban sprawl in the Central Valley.

However, as reviewed by Rolfe (2001), NCCPs and HCPs have significant shortcomings and incongruous objectives due to their reliance on take permits under FESA Section 10(a) and CESA Section 2835. Simply put, the FESA and CESA are reactive responses to species in jeopardy of extinction, while regional conservation plans are ostensibly a proactive approach to prevent the decline of species in the first place (Rolfe 2001). While NCCPs aim to promote multispecies and multihabitat management and the conservation of broad-based natural communities and species diversity, the impetus to initiate one is typically the conservation of listed or potentially listed species.

County general plans and ordinances are another important yet underutilized tool to conserve peripheral populations and other locally significant species and habitats. Santa Cruz County, for instance, has a "Sensitive Habitats Protection Ordinance" that requires that no development activities or land disturbance that results in disturbance to ". . . locally unique plants and animals or their habitats" can occur until a biotic review is conducted and necessary mitigation measures are developed to protect the habitat (Santa Cruz County Planning Department 2005). The Ventura County, California General Plan specifies that "locally important species/communities" are a significant biological resource to preserve and protect (Ventura County 1988).

Millar and Libby (1991) suggest that important populations of widespread species be conserved, in part, by the creation of "genetic resource management units" (GRMUs). These GRMUs can be, in essence, wilderness areas, botanical areas, or lands covered by a NCCP/HCP, if their management objective is the *in situ* conservation of biodiversity at the regional genetic-variation level. We agree with Millar and Libby (1991) on the necessity of creating GRMUs to conserve regional genetic diversity, and we recognize that simply by protecting large areas, NCCPs and HCPs can also protect significant peripheral populations. However, the full potential of regional conservation plans and other designated conservation areas in protecting regionally significant peripheral populations cannot be realized until their importance is better appreciated, actual populations are identified, and most importantly, their conservation priority is integrated into the management objectives of these regional plans.

Currently, there are 22 NCCPs being developed in California and nine that have been approved and permitted. All of these NCCPs are joined with an HCP and are typically 50-to 80-year agreements. Together, these 31 NCCPs cover over seven million acres (28,328 km^2), representing approximately seven percent of California. This is, therefore, a propitious time to emphasize the significance of peripheral populations during regional planning.

Need for more Accurate Delineation of Local Floras

Closer scrutiny of local floras and phytogeographic patterns is required to identify peripheral populations having significant conservation value. A principal impediment to the conservation of locally significant peripheral populations is the relative absence of finer-scale data on species distributions. Presently, the general geographic distribution of common species, such as those not tracked by CNPS, is understood only at the county-level scale, (for example Munz 1959, 1968), and therefore is of limited use in conservation planning because the spatial scale is too coarse.

Recently, however, CNPS chapters and others have begun compiling regional lists of peripheral, disjunct, or what has been termed "locally rare" taxa, in an effort to conserve them (Lake 2004; Magney 2004). Other regional and county floras (such as Thomas 1961; Hoover 1970; Smith and Wheeler 1992), although outdated, provide important data on peripheral populations (many now extirpated). Thomas (1961), for instance, lists 181 taxa with their southern geographic limits and 61 taxa with their northern limits in the Santa Cruz Mountains. We encourage the continued documentation and compilation of local floras and peripheral populations and otherwise regionally significant plant lists as a first step in understanding their conservation value and protecting them where appropriate.

Local floras are also important tools for identifying where concentrations of regionally and locally significant populations occur (i.e., biodiversity hotspots, potential reserve sites,

and finer-scale ecological boundaries) (Araujo 2002; Leppig 2004). Heckard and Hickman (1984), for example, demonstrate how a detailed local flora can highlight the conservation significance of a location due to its high concentration of peripheral plant populations. In the absence of more-spatially explicit data on plant species distributions, locally significant peripheral plant populations will continue to be unknowingly extirpated with no attempt to conserve them.

Lastly, the variation in size of county-level political units—both within California and among states—hampers effective comparative analyses and uniform application of conservation criteria. To ameliorate this problem, we advocate the use of methodologies based on 5 km × 5 km grids for characterizing plant distributions. Although some limitations and cautionary notes should be considered when using these methodologies (White 1999, 2004), they have been used effectively elsewhere (IUCN 2001; Pearman and Dines 2002) to accurately describe plant spatial patterns.

Summary Considerations

The evolutionary significance—and therefore conservation value—of peripheral populations is well documented, as is the greater threat of their extirpation. However, in our opinion, their value has yet to enter the zeitgeist of the conservation community. Peripheral populations have remained, at best, a marginal component of conservation planning since Millar and Libby (1991) first called attention to the conservation of significant populations of widespread species 15 years ago. In this paper, we emphasize populations rather than taxa, genetic diversity over taxonomic diversity, and evolutionary potential and processes over floristic maintenance. Thus, we have attempted to change how conservationists view rarity and commonness, and the scale and structure at which rarity typically is assessed. We hope to have also stimulated discussion and debate on this subject.

Our goal here is not to throw out the existing conservation structure, with its emphasis on listed, endangered, and narrowly endemic species, but rather to shift the conservation paradigm to include a different and typically overlooked suite of rare plants—those on the frontiers of their range. Endangered species and species rare throughout their range should, of course, be accorded high conservation priority. However, to optimize conservation planning and the long-term persistence of floristic diversity, conservationists also need to look beyond rare and endangered species and their habitats. Not all peripheral populations are worthy of conservation, but many clearly are. Identifying which populations warrant conservation efforts poses a continuing challenge. More genetic data, a better understanding of how metapopulation theory applies to these populations, and an even more-explicit approach than we present here for assessing conservation significance will clearly help.

We acknowledge that conservation resources are scarce, and will likely remain so. However, in our view, placing greater conservation emphasis on certain important peripheral populations will not necessarily take scarce resources away from species in perhaps greater need; rather, it will enhance current conservation efforts and large-scale regional planning.

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THE ARBUCKLE-HERSHEY CHAMISAL (*ADENOSTOMA FASCICULATUM*): A SIGNIFICANT ANOMALY IN CALIFORNIA PLANT GEOGRAPHY

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ABSTRACT

In a 1922 monograph on the California chaparral, William S. Cooper called attention to some patches of chamise (*Adenostoma fasciculatum*) growing robustly on deep alluvial soils on the west side of the lower Sacramento Valley. He submitted that these patches were relicts of "the true regional climax," suggesting that centuries of Indian burning accounted for the prevalence of grass instead of brush when the Sacramento Valley was first seen by Europeans. We examined available historical evidence and found that Cooper was right in concluding that the chamise patches he saw were vestiges of a much more extensive (ca. 4000 ha) aboriginal stand. Whether the controlling local influence was edaphic or anthropogenic, and whether the local pattern had any wider regional implications, are questions that remain open to speculation.

Key Words: California chaparral, California valley grassland, Sacramento Valley, relict evidence, historical vegetation mapping.

More than 80 years ago, in a seminal monograph on the California chaparral, ecologist William S. Cooper (1922) called attention to what he deemed "a very interesting and significant bit of relict evidence." He had found some well-developed patches of *Adenostoma fasciculatum* Hook. & Arn. (Rosaceae) on deep alluvial soils on the west side of the lower Sacramento Valley, between the towns of Arbuckle and Hershey. He thought the fact that *A. fasciculatum* and associated brush species could grow to full size and form a solid cover "under typical valley conditions" indicated that these patches were "almost certainly relicts of former dominance rather than centers of recent colonization," and likely represented "the true regional climax." He supposed that longtime burning by Indians accounted for the general prevalence of grass, not brush, when the Sacramento Valley was first seen by Europeans. This suggestion ran counter to the ascendant view of Frederic Clements (1920), who posited that grassland (especially *Nassella* spp.) represented the true climax vegetation of the Sacramento Valley.

Cooper's interesting hypothesis still garners mention in the plant ecology literature of the region (Hamilton 1997; Keeley 2000). It has been cited approvingly by those who maintain that aboriginal burning was a primary factor in the evolution of the California landscape (Stewart 2002). However, neither supporters nor scoffers have investigated the historical background of the presumed relicts Cooper saw ca. 1920. Utilizing mile-by-mile descriptions of land cover by a U.S. General Land Office surveyor in 1853, we have pieced together a map of the Arbuckle-Hershey locale's vegetation as it existed prior to modern agricultural conversion.

The government surveyor, James R. McDonald, encountered a landscape as yet only lightly disturbed by agricultural settlers—only five 64-ha preemptors were established in nine survey townships (83,000 ha) when he was here in September-October 1853 (U.S. General Land Office 1853). McDonald found no settlers at all in township 13N-2W (9200 ha), the heart of which was dominated by brush he called "greasewood," which he described as "almost impenetrable." This "dense thicket" was evidently well known to local people as late as 1872 (Rogers 1891). Specimens of *A. fasciculatum* from here were vouchered by Alice King in 1906 and Harvey Hall in 1919 (UC/JEPS 2005)—it was at Hall's urging that Cooper's attention was directed to this locale. However, by the time the land was subdivided for orchard and vineyard planting ca. 1911, nearly all the brush had been cleared and the land for many years devoted to wheat and sheep (Superior California Fruit Land Company [1911?]). Nothing was said about it in soil surveys of the area conducted in 1909 and 1942–1945 (Mann et al. 1911; Harradine 1948). Today, land use in this area is characterized by a near-monoculture of irrigated almond orchards, and a visitor must search hard to find even a single specimen of *A. fasciculatum*.

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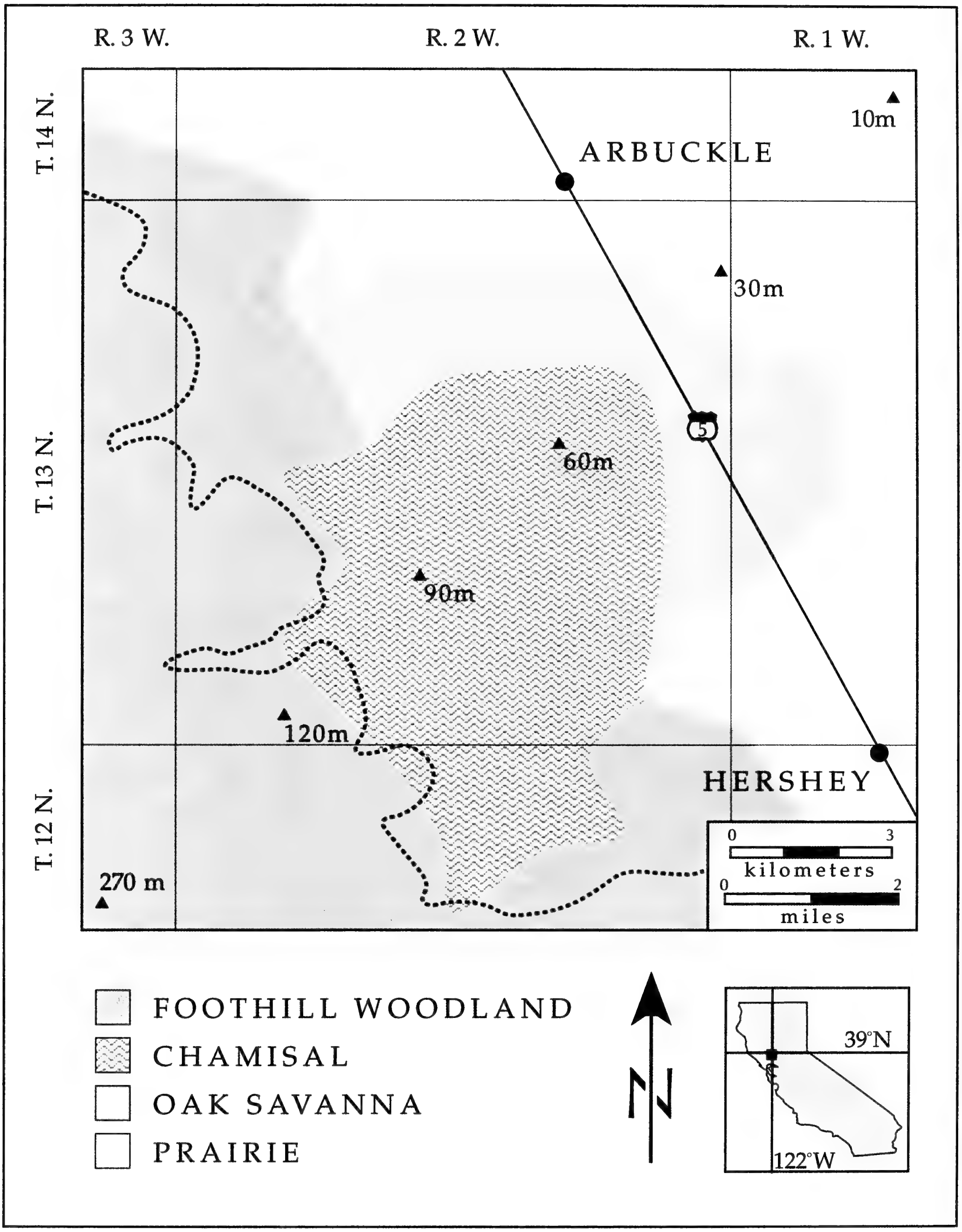

FIG. 1. Presettlement vegetation cover of the Arbuckle-Hershey vicinity, Colusa and Yolo counties, California. Centered on U.S. public land survey township 13N 2W, Mt. Diablo base line (U. S. General Land Office 1853). Dashed line indicates upper edge of Sacramento Valley alluvium (Wagner and Bortugno 1982). Virtually everything east of this line is cleared and farmed at present. "Foothill woodland" = *Quercus douglasii* + *Pinus sabiniana*; "Chamisal" = *Adenostoma fasciculatum*; "Oak savanna" = *Q. douglasii*; "Prairie" = "bunch grass" (*Nasella* spp.?) + *Avena* spp.

Our reconstruction from McDonald's 1853 survey field notes (Fig. 1) reveals a compact stand of chamise (*A. fasciculatum*) covering some 4000 ha. Above it, to the west and southwest, was typical California foothill woodland: *Quercus douglasii* Hook. & Arn. (Fagaceae) and *Pinus sabiniana* Douglas (Pinaceae) with an understory of *A. fasciculatum* and various broad-leaved chaparral species. Around the lower, easterly margin of the chamisal was a halo of *Q. douglasii* savanna. Below that was "prairie," described by McDonald as "bunch grass" (*Nassella* spp.?) and "wild oats" (*Avena* spp.). McDonald observed that the prairie was being invaded by "weeds," species not indicated.

An edaphic influence suggests itself when we compare the 1853 vegetation pattern with maps of local geology and soils, yet questions remain. Foothill woodland was clearly associated with late Pliocene and early Pleistocene structures of the Tehama and Red Bluff formations, and their peripheries. The chamisal and *Q. douglasii* savanna were associated with late Pleistocene alluvium of the Modesto-Riverbank Formation (Wagner and Bortugno 1982). They were centered on, but neither coextensive with nor limited to, soils of the Hillgate-Arbuckle-Corning association (Reed 2002). These soils (Xeralf suborder) are generally characterized by a coarse-textured upper horizon (>20 percent fine gravel and coarse sand) underlain by compact gravelly clay loam; reaction is slightly acidic (pH 5.8–6.4); relief is level to moderately sloping (0–5 percent).

Cooper was right in concluding that the *A. fasciculatum* patches he saw in the Arbuckle-Hershey locale ca. 1920 were "relicts of former dominance" over a substantially wider area. However, his deduction that such fragments indicated a "true" control by chamisal of the Sacramento Valley is still open to argument. Was the local pattern edaphic? The Hillgate-Arbuckle-Corning soil association is extensive on the west side of the Sacramento Valley, but we have found no evidence that the peculiar sequence of vegetation types described here occurred anywhere else in the region ca. 1853. Was it anthropogenic? Cooper thought the region's potential brush cover had been "pushed back" and "pinched out" by centuries of Indian burning, but the long-standing consensus among California range managers is that *A. fasciculatum* stands are persistent, even aggressive, in the face of repeated fires (Sampson 1944).

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A NEW CLUB CHOLLA, *GRUSONIA ROBERTSII* (CACTACEAE) FROM BAJA CALIFORNIA SUR, MEXICO

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ABSTRACT

A new species of club cholla (**Grusonia robertsii**) endemic to the Vizcaíno Desert of Baja California Sur is described here for the first time. Distribution, associated vegetation, rarity, affinities to other related species, a botanical illustration, a key to the species in the genus *Grusonia* of the Lower California region, and a key for the generic reclassification of *Opuntia* sensu lato as recognized by Wiggins (1980) but currently treated as three different genera in the region are also presented.

RESUMEN

Se describe aquí por primera vez una especie nueva de casa rata (*Grusonia robertsii*) endémica del Desierto Vizcaíno, del estado de Baja California Sur. Se presentan la distribución, vegetación asociada, rareza, afinidad con otras especies en el género, una ilustración del nuevo taxón, una clave a las especies en el género *Grusonia* de la península de Baja California, y una clave para la reclasificación genérica de *Opuntia sensu lato* de Wiggins (1980), que actualmente es tratada como tres géneros diferentes en esta región, y que también se presentan aquí.

Key Words: Cactaceae, *Grusonia*, *Corynopuntia*, Baja California Sur, Mexico.

Lower California is comprised of two Mexican states (Baja California and Baja California Sur) that are politically divided at the 28th parallel. These states comprise the Baja California peninsula and its adjacent islands located in both the Gulf of California (Sea of Cortés) and the Pacific Ocean. This region supports a wealth of plant species diversity. Wiggins (1980) estimated that 2958 total taxa including 686 endemic taxa occur in Lower California or an endemism rate of 23.2%, but recent plant discoveries and a more complete overview of the literature suggests that the flora consists of more than 4000 plant taxa with a rate of endemism closer to 30% (Rebman 2001). The Cactaceae are a conspicuous and diverse component in most areas and plant communities of Lower California. According to Rebman (2001), the Cactaceae of Lower California are represented by 15 genera, 104 species, and 129 total taxa. Of these, 71 species and 92 taxa are endemic to the region, a 68.3% endemism rate for species and 71.3% for taxa. The genus *Opuntia* Miller sensu lato (including *Grusonia* Britton & Rose [*Corynopuntia* F. M. Knuth to some authors], *Cylindropuntia* (Engelm.) F. M. Knuth, and *Opuntia* sensu stricto) was considered to have the highest number of overall taxa (41) in the region before it was split into three genera (Anderson 2001). Only two species in the genus *Grusonia* (*G. invicta* (Brandegee) E. F. Anderson and *G. kunzei* (Rose) Pinkava) were previously known to occur on the peninsula of Baja California.

Grusonia robertsii *Rebman*, sp. nov. (Fig. 1)

Type. MEXICO, Baja California Sur: Vizcaíno Desert near 27°19′N, 113°08′W, between San Ignacio and Guerrero Negro, 28 October 2001, *Rebman 7795* (holotype: SD 148287; isotypes: ASU, BCMEX, HCIB).

Paratypes. MEXICO, Baja California Sur: Vizcaíno Desert, between San Ignacio and Guerrero Negro, 10 May 1992, *Rebman 1361* (ASU 187542, SD 155542); 10 March 1998, *Rebman 4836 & N. Roberts* (SD 143343).

Note. The specific locations of this new cactus species including detailed latitude and longitude coordinates have been intentionally omitted due to the lack of known populations, its rarity in the field, and the popularity that cacti have in the hobby/horticultural industry.

Latin diagnosis. Grusonia kunzei (Rose) Pinkava simile, sed differt fructibus brevioribus 20–35 mm longis, areolis per fructum paucioribus (25–30), et spinis majoris caulinis complanatis leviter basi.

English diagnosis. This species resembles *Grusonia kunzei* but differs in having a shorter fruit, 20–35 mm in length, fewer areoles (25–30) per fruit, and major spines of the stems only slightly flattened at the base.

Shrubs, low to nearly mat-forming, to 45 cm tall. **Stem** segments succulent, 7.5–11 × 2.5–3.5 cm (Fig. 1A); tubercles prominent, 20–35 ×

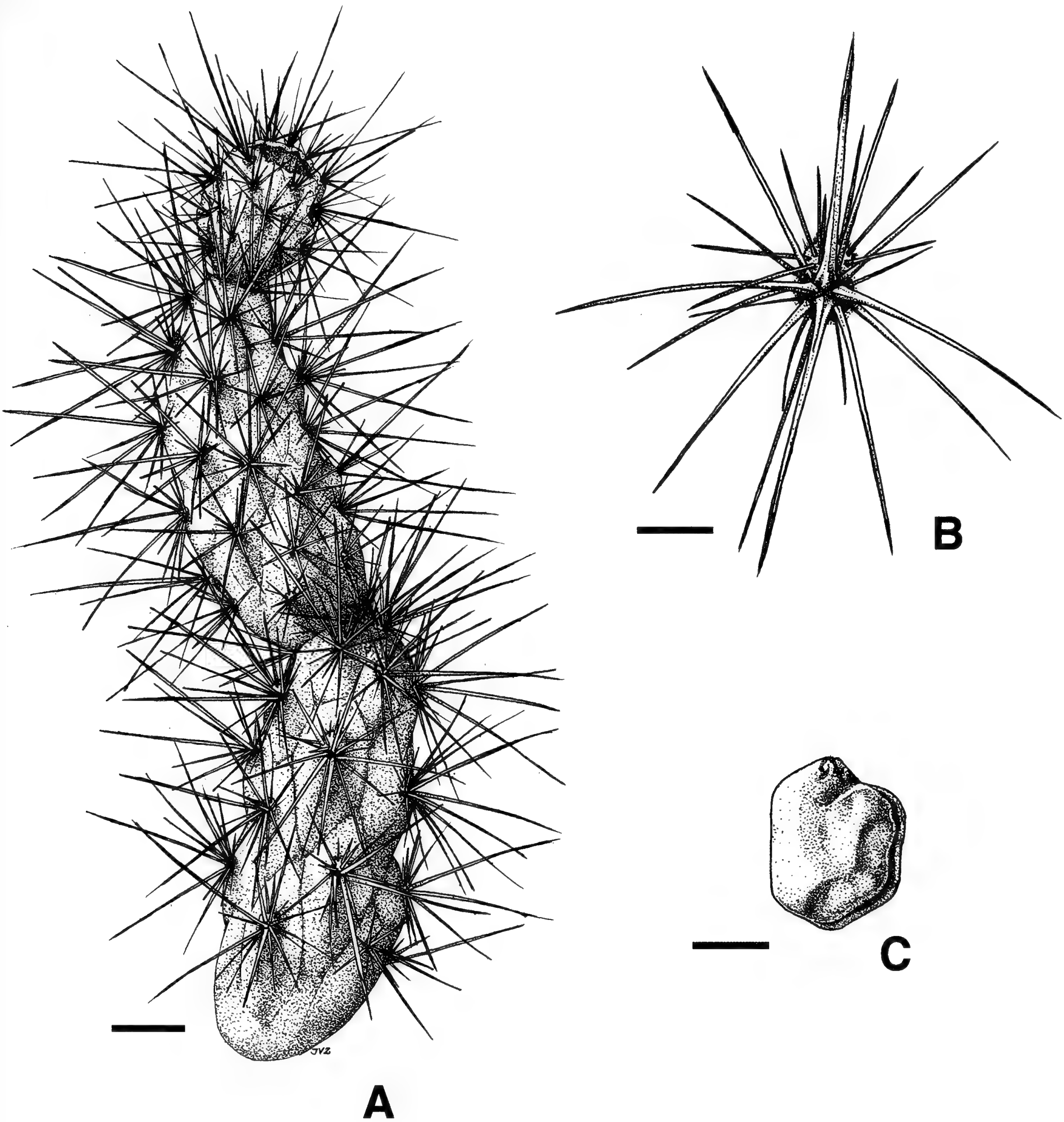

FIG. 1. *Grusonia robertsii*, showing terminal stem segments and immature fruit with long, deciduous glochids (A), measurement bar = 2 cm; stem areole with spines (B), bar = 1 cm; seed (C), bar = 2 mm.

5–13 mm. **Areoles** 6–7 × 4–6 mm with cream to gray wool. **Spines** 12–20 per areole (Fig. 1B), lavender-gray (yellowish on one individual), uniformly distributed along the stem, the central, major ones 3–4, divergent, slightly flattened to strongly angled at base, 0–4 sheathless, bristle-like spines. **Glochids** in a sparse, apical crescent on stem areoles, gray to dark brown, 2–9 mm; fruit and flower areoles with an apical crescent of cream to light yellow glochids, 2–6 mm; plus in flower areoles other glochids are present, orange-brown to gray, up to 25 mm long. **Flowers** yellow; filaments green; styles greenish-yellow. **Fruits** sub-spheric to short turbinate, 20-35 × 15–22 mm with 25–30 areoles; covered with long, deciduous glochids when young but at maturity, mostly spineless with up to 7 spines strongly attached in some scattered areoles; yellow and fleshy when ripe. **Seeds** 25–35 per fruit, 3–4.5 mm in diameter (Fig. 1C).

Distribution and Habitat. Endemic to Baja California Sur; individuals of *Grusonia robertsii* occur on flat plains and lower slopes of volcanic mountains in coarse sandy substrates scattered with large basaltic rocks; elevation 120–240 m;

Vizcaíno Desert associated with a succulent desert scrub dominated by *Yucca valida* Brandegee, *Pachycereus pringlei* (S. Watson) Britton & Rose, *Fouquieria diguetii* (Tiegh.) I. M. Johnst., *Bursera microphylla* A. Gray, *Stenocereus gummosus* (Engelm.) Gibson & Horak, *Grusonia invicta*, *Cylindropuntia cholla* (F. A. C. Weber) F. M. Knuth, and *Echinocereus brandegeei* (Coulter) K. Schum. Additional associates include: *Atriplex barclayana* (Benth.) D. Dietr., *Cylindropuntia alcahes* (F. A. C. Weber) F. M. Knuth, *Euphorbia misera* Benth., *Ferocactus peninsulae* Britton & Rose, *Frankenia palmeri* S. Watson, *Lophocereus schottii* (Engelm.) Britton & Rose var. *schottii*, *Mammillaria dioica* K. Brandegee, *M. lewisiana* Gates, *Pedilanthus macrocarpus* Benth., *Stenocereus thurberi* (Engelm.) Buxbaum, and *Tillandsia recurvata* L.

Phenology. Flowers in May; fruits persist on plant until at least November.

Etymology. This new cactus is being named in honor of Dr. Norman Roberts, a friend, naturalist, and explorer of the deserts in Lower California. Dr. Roberts has contributed immensely to our knowledge and enjoyment of plants in Lower California by publishing a book entitled "Baja California Plant Field Guide" (Roberts 1989), and by promoting and facilitating botanical studies and explorations in the region.

Discussion

Grusonia robertsii, found in the Vizcaíno Desert of northern Baja California Sur, is a rare, but distinct new club cholla. Although it grows sympatrically with *G. invicta*, it appears to be most closely related to *G. kunzei*, which is found in southwestern Arizona, Sonora and approximately 450 km to the north in the San Felipe Desert of Baja California.

In 1992, when I discovered the first individual of *Grusonia robertsii*, I originally thought it to be a naturally occurring, intergeneric hybrid between *Grusonia invicta* and *Cylindropuntia alcahes*. Interspecific hybridization is a common occurrence in the Cactaceae, especially in the genus *Cylindropuntia*, and has played an integral part in the evolutionary process of the family (Pinkava et al. 1998). However, after closer morphological evaluation and after the discovery of other individuals in the population at the type locality over the years, I have determined it to be a new, rare species in the genus *Grusonia*. Although only six individuals of this new species have yet been recorded, it does not seem to be of hybrid origin. This new taxon has spine sheaths deciduous only at the spine apex, major spines that are flattened to angled at the base, areoles of flowers and fruits with longer tufts of wool, and a low-growing habit; all are characteristics of the genus *Grusonia*. However, the shape of the fertile fruits is not like other known species in the genus, which is usually narrowly obconic to ellipsoid. In fact, the fruit of this new species is more similar to that found in various species of the genus *Cylindropuntia* which are short-turbinate to subspheric. It should be noted that there are no known hybrids between the opuntioid genera *Cylindropuntia* and *Grusonia*, and that the high seed set in the fruits of this new taxon would seem to indicate that it is reproducing by seeds.

Part of the reason for its paucity of field observations and collections is due to the difficulty in differentiating this new species from other sympatric cacti at a distance. It is convergent in growth habit to *Grusonia invicta* and to *Echinocereus brandegeei*, both of which are common species in the vegetation of the type locality. All three species are low-growing to mat-forming shrubs that are densely shrouded with gray spines and without close inspection, the vegetative parts of these species are readily confused. Although *E. brandegeei* has bright yellow, acicular spines in much of its distribution, it has gray, flattened spines in the region of the peninsula near San Ignacio. In truth, I have visited the type locality for *G. robertsii* at least six different times and almost each visit has revealed a new individual in the population (the last time with five separate individuals observed was in October 2001). Because the vegetation and habitat in which this new species occurs is quite widespread in this part of the peninsula, it is probable that this new club cholla is more common than is currently known. As a matter of fact, during a trip to the region in January 2005, I observed another individual plant (a yellow-spined form) of this new species almost 30 km southeast of the type locality. Conversely, there are other cacti on the peninsula such as *Echinocereus lindsayi* J. Meyran that also occur in a widespread habitat and vegetation type of the Vizcaíno Desert that are very rare indeed, which might also be the case for this new species.

Key to the Species in the Genus *Grusonia* in Lower California

1. Stems subspherical, length < 2 times width; flowers with reddish filaments . . . . *G. invicta* (Brandegee) E. F. Anderson.

1′. Stems cylindric-clavate, length > 2 times width; flowers with yellow to green filaments.

2. Fruit very spiny, narrowly ellipsoid to cylindric, 40–75 mm in length, with 40–70 areoles, major spines of stem areoles strongly flattened; occurs in Arizona, Sonora and northern Baja California . . . . *G. kunzei* (Rose) Pinkava.

2′. Fruit naked to sparsely spiny, short turbinate to subspheric, 20–35 mm in length, with 25–30 areoles; major spines of stem areoles mostly angled to slightly flattened at base; known

only from northern Baja California Sur . . . .
. . . . *G. robertsii* J. Rebman.

Separation of the Genus *Opuntia Sensu Lato*

The large genus *Opuntia* sensu lato is currently being recognized (Anderson 2001) as various smaller, segregate genera. In Lower California, the genus *Opuntia* s.l. as recognized by Wiggins (1980) is now treated as three different genera: *Grusonia* (or *Corynopuntia* for some authors), *Cylindropuntia*, and *Opuntia* s.s. These three genera can easily be distinguished based upon vegetative morphology such as stem shape and spine characters.

Key to the Genera of Lower California Previously Recognized as *Opuntia Sensu Lato*

1. Stem segments cylindric to clavate; spines variously sheathed (at least when young).
   2. Stem segments cylindric; trees or shrubs, erect to decumbent or trailing but not mat-forming; spine sheaths covering entire spine and sometimes long-persisting; spines round in cross-section . . . . *Cylindropuntia* (chollas).
   2′. Stem segments clavate to spheric; shrubs, low, mat-forming or caespitose; spine sheaths only covering spine tips and usually quickly deciduous; most major spines flattened in cross-section . . . . *Grusonia* (club chollas).

1′. Stem segments flattened into cladodes or rarely subcylindric; spines sheathless. . . . . *Opuntia* (prickly-pears, nopales).

Acknowledgments

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TRICHOSTEMA RUYGTII (LAMIACEAE): A NEW SPECIES FROM NAPA COUNTY, CALIFORNIA

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ABSTRACT

Trichostema ruygtii is described from Napa County, California. It is closely related to *T. lanceolatum* Bentham but differs from that species most conspicuously in having much smaller flowers with notably shorter stamens. Both species occur in Napa County but occupy somewhat different habitats and have not been found growing together.

Key Words: Lamiaceae, California, new species, *Trichostema ruygtii*, *Trichostema lanceolatum*.

Jake Ruygt, who is writing a flora of Napa County, California, wrote to me in the summer of 2003, asking for help in the identification of a species of *Trichostema*. He had been reporting locations of this plant to the California Natural Diversity Database for a number of years as *Trichostema rubisepalum*, a rare species known only from the foothills of the Sierra Nevada in Tuolumne and adjacent counties and a small disjunct area in San Benito County. The identification had been made by Joe Callizo, a knowledgeable local botanist, 20 or more years ago and had not been questioned until Mingjuan Huang, a Ph.D. student at Ohio State University, referred to these plants in her studies as *T. lanceolatum* based on my identification of a pressed specimen she sent to me in 1997.

Faced with alternative names, Jake Ruygt compared his material with collections at University of California Berkeley and with living populations of *T. lanceolatum*. He became convinced that the plants he had been reporting as *T. rubisepalum* were not that species and that they did not appear to be *T. lanceolatum* either. The photographs he enclosed suggested that further study was desirable and at my request he sent me pressed specimens from five populations. Although numerous morphological similarities indicated a very close relationship to *T. lanceolatum*, consistent floral differences convinced me that the questioned plants represented a distinct undescribed taxon.

Because floral traits are difficult to measure in pressed specimens of this and related taxa, I suggested to Jake Ruygt that he make additional field observations during the next flowering season and measure appropriate samples of living material from several different populations including at least one Napa County population of *T. lanceolatum*.

Since Jake Ruygt not only brought attention to the problem but provided all of the field observations and measurements of living plants from Napa County, I take pleasure in naming this species for him.

Trichostema ruygtii H. Lewis, sp. nov. (Fig. 1).—TYPE: California, Napa County. Mead Ranch, 2.4 km southwest of Foss Valley, *J. Ruygt 3089*, 11 July 1992. Opening in chamise chaparral. Elevation 475 m. (Holotype: JEPS; Isotypes: CAS, LA, RSA, MO).

A *Trichostemate lanceolato* Benth. staminibus minus quam 10 mm longis et stigmatibus non exsertis ultra antheras differt.

Erect annual herb to 50 cm tall, unbranched or with ascending branches in the lower half; stem and leaves viscid with capitate glands and pubescent with short curved hairs and straight spreading hairs to 2 mm long; leaves sessile or nearly so, blade lanceolate, 1–4 cm long, 2–10 mm broad, creased along the midrib, apex acute and generally pungent, base rounded or acute, ascending lateral veins arising near the base and appearing nearly parallel are usually evident on the lower surface of larger leaves; inflorescence secund with axillary racemes to 1 cm long with 1–10 flowers; pedicels 1–3 mm long; calyx in flower 3–5.5 mm long increasing to 4.2–7.5 mm in fruit, lobes deltoid to lanceolate, acute or pungent, generally equal to or somewhat shorter than the tube, the uppermost slightly narrower than the lower 4; corolla tube 5–7.5 mm long, exserted 1–3 mm beyond the calyx, curved upward and sharply bent back as the tube narrows near the throat; lower lip 2–4.5 mm long, white with numerous purple spots; lateral lobes 1.5–4 mm long, blue-violet, pinkish or white, the upper lobes erect, generally longer than the lower, the lower lip reflexed, usually speckled with purple; stamens exserted, arched, 5–9.5 mm long, anthers about 1 mm long; stigma opposite or below the anthers; nutlets alveolate with ridges and projections, 1.8–3.2 mm long, about 1.8 mm broad.

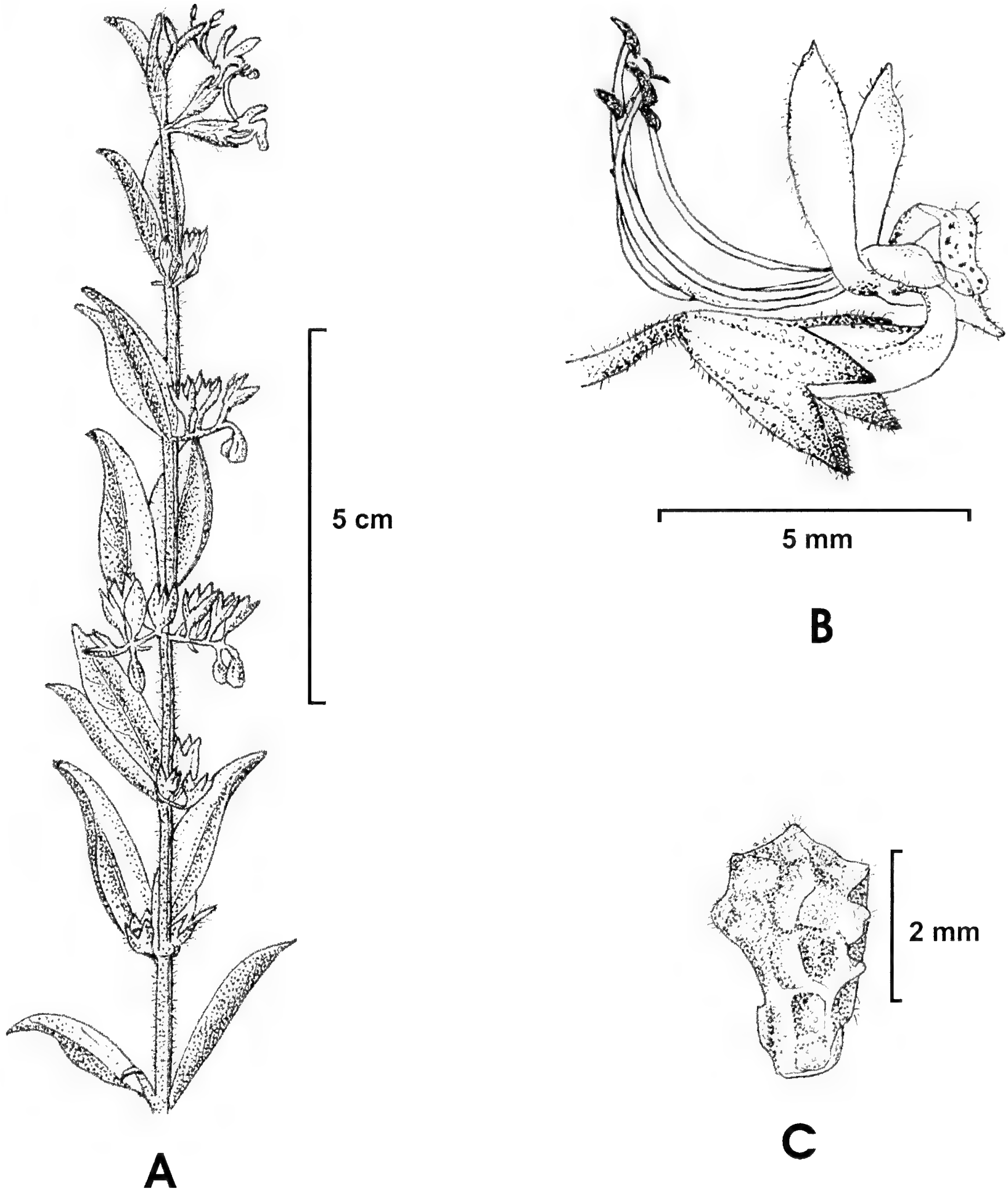

FIG. 1. *Trichostema ruygtii.* A. Habit. B. Flower. C. Nutlet.

Trichostema ruygtii flowers from June to October in open sunny areas associated with a variety of vegetation types, primarily oak woodland with various species of oaks, but also chaparral, grassland (former woodland) and yellow pine-Douglas fir forest. It is generally found on thin clay soils on dry rocky slopes and flats that are often adjacent to exposed volcanic bedrock of the Sonoma Volcanic Formation. Some sites are seasonally saturated, including Northern Volcanic vernal pools.

Populations are known from 19 localities in the Napa Range and eastern interface with Napa Valley at elevations of 30 to 600 m (Fig. 2). Fifteen of these are documented by collections and four others are based on recent observation of populations not far from documented sites.

Type. California, Napa County. Mead Ranch, 2.4 km southwest of Foss Valley, *J. Ruygt 3089*, 11 July 1992. Opening in chamise chaparral.

Elevation 475 m. (Holotype: JEPS; Isotypes: CAS, LA, RSA, MO).

Documented locations: 2.4 km southwest of Foss Valley (Mead Ranch), *Ruygt 3089*; 3 miles NE of Napa, 1.9 km SE of intersection of Third Avenue and Hagen Road, *Ruygt 4628*; Soda Canyon Road, 0.5 km north of Loma Vista Dr.,

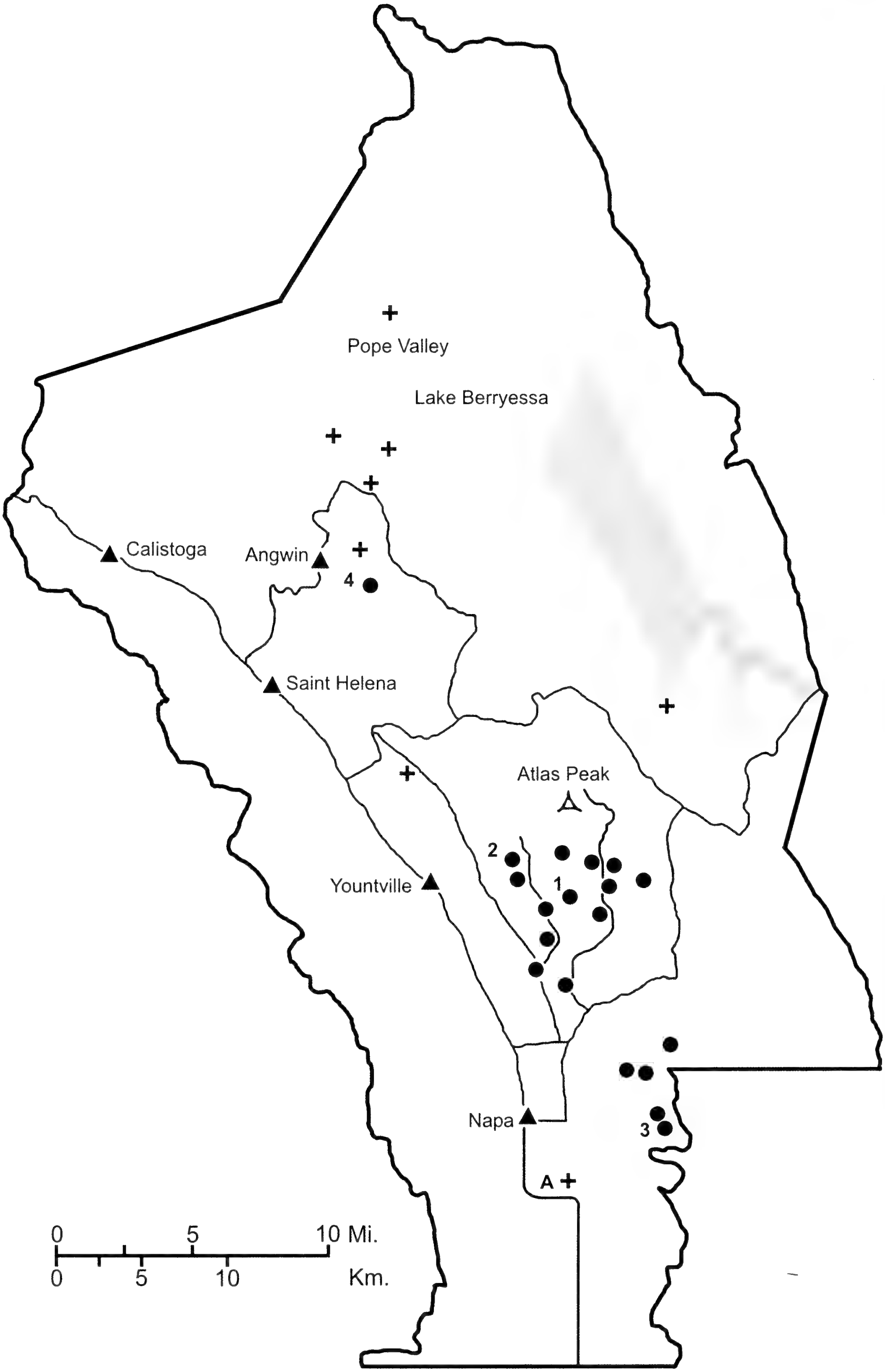

FIG. 2. Distribution of *Trichostema ruygtii* (●) and *T. lanceolatum* (+) in Napa County, California.

TABLE 1. LOCATIONS OF SAMPLED POPULATIONS AND VOUCHER COLLECTIONS.

Trichostema ruygtii
1. 2.4 km southwest of Foss Valley (Mead Ranch), *Ruygt 3089* (Type locality)
2. North end of Stag's Leap, *Ruygt 4644*
3. East end of Green Valley Road, 0.89 km west of Wild Horse Falls, *Ruygt 4640*
4. Las Posadas State Forest, northwest of fire station, *Ruygt 2808*

Trichostema lanceolatum
A. Napa County, 5.1 km S of Napa (Courthouse), east side of Napa Valley Corporate Road, *Ruygt 4649*
B. Los Angeles County, Santa Monica Mountains National Recreation Area, Mulholland Highway, 1.6 km east of Malibu Canyon/Las Virgenes Road, *H. Lewis 1480*

Ruygt 4632; Atlas Peak Rd., 11.4 km north of Monticello Rd. (Foss Valley), *Ruygt 737*; Buzzard's Roost, 0.5 km east of Stag's Leap, 5 km ENE of Yountville, *Ruygt 4638*; north end of Stag's Leap, *Ruygt 4644*; east of end of Green Valley Road, 0.9 km west of Wild Horse Falls, *Ruygt 4640*; Las Posadas State Forest, NW of fire station, *Callizo*, 11 Aug. 1985; *Huang*, 12 Aug. 1997; *Ruygt 2808*; Atlas Peak Rd., 6.8 km north of Westgate Drive, 0.9 km SSE of Foss Valley, *Ruygt 1855*; Atlas Peak Rd., 0.5 km north of Hardman Ave., *Ruygt 4648*; Soda Springs Rd., 0.5 km east of Soda Canyon Rd., *Ruygt 4666*; near Circle Oaks, on ridgetop 1.5 km west of "Munson Ranch", *Ruygt 4677*; Wild Horse Valley Ranch, 1.4 km north of Lake Madigan, *Ruygt 3062*; NW Foss Valley (Antinori Vinyards), 3.1 km SSW of Atlas Peak, *Ruygt 4433*.

Other locations: West of Milliken Reservoir near Atlas Peak Road; Soda Canyon Road, 0.4 km north of Silverado Trail; northeast of Napa, Third Avenue at Napa Valley Country Club, 0.9 km SE of intersection of Third Ave. and Hagen Road; SE Foss Valley, 1.2 km SE of Atlas Peak schoolhouse.

Although all recent collections and observations have been made in Napa County, *T. ruygtii* may occur in adjacent counties. The Wild Horse Valley to Twin Sisters area in Solano County seems promising and a collection from Lake County is known. This collection by Pauline Schulthess, July 15, 1931, on a ranch 2.4 km southwest of Kelseyville (LA, UC) is about 60 km NW of the closest known population of *T. ruygtii* in Napa County. A recent survey of the area disclosed three populations of *T. lanceolatum* but no trace of *T. ruygtii*, which may have been extirpated by development in the area since 1931.

Based on observations and measurements of living populations (Table 1) supplemented by data for *T. lanceolatum* from an earlier study of herbarium specimens (Lewis 1945), there can be little question of a very close relationship between *T. ruygtii* and *T. lanceolatum*, the most widely occurring species of the genus in western North America. *Trichostema ruygtii* is scarcely distinguishable in habit and vegetative characteristics from *T. lanceolatum* and the flowers of both species are similar in having an unusual conformation of the corolla, with the corolla tube bending back sharply as it narrows near the throat. However, except for the calyx and ovary, the flowers of *T. lanceolatum* are conspicuously larger (Table 2) with notably longer stamens that have larger anthers, about 1.5 mm long. The species also differ in the position of the stigma, which is exserted 1–2 mm beyond the anthers in *T. lanceolatum* and not exserted in *T. ruygtii*. These differences are correlated with seed set, which Ruygt observed to be high in *T. ruygtii*. His data from 20 plants at the type locality (Population 1, Table 1) gave a value of 87% whereas Spira (1980) reported 44% for *T. lanceolatum* and my data from Population B (Table 1) gave 49%. Differences in proportions are also evident (Table 3).

The small flowers of *Trichostema ruygtii*, the position of the stigma, and a high seed set suggest to me that it is a self-pollinating derivative of *T.*

TABLE 2. *TRICHOSTEMA* FLOWER MEASUREMENTS. Measurements in mm: mean ± standard deviation. Sample size: Populations 1, 2, 3, 4, and A = 20; B = 15.

		Calyx		Corolla				
		Total	Lobe	Tube	Upper lobe	Lower lobe	Lip	Stamens
T. ruygtii	1	4.35 ± 0.39	1.91 ± 0.39	6.05 ± 0.48	2.43 ± 0.34	2.24 ± 0.33	3.35 ± 0.59	6.50 ± 0.74
	2	4.54 ± 0.39	2.26 ± 0.36	6.08 ± 0.52	2.78 ± 0.30	2.68 ± 0.37	3.14 ± 0.47	7.68 ± 0.60
	3	4.90 ± 0.44	2.33 ± 0.41	6.72 ± 0.47	3.24 ± 0.26	3.03 ± 0.28	3.81 ± 0.63	7.78 ± 0.55
	4	4.12 ± 0.34	1.58 ± 0.27	5.93 ± 0.54	2.48 ± 0.35	2.37 ± 0.30	3.54 ± 0.34	6.90 ± 0.64
Species mean		4.48 ± 0.39	2.02 ± 0.36	6.20 ± 0.50	2.73 ± 0.31	2.58 ± 0.32	3.46 ± 0.51	7.46 ± 0.63
T. lanceolatum	A	3.94 ± 0.51	1.69 ± 0.59	8.19 ± 0.71	5.62 ± 0.68	4.18 ± 0.59	5.28 ± 0.72	16.47 ± 1.09
	B	5.31 ± 0.56	2.90 ± 0.54	6.71 ± 0.99	6.10 ± 0.78	4.97 ± 0.62	6.27 ± 0.94	19.73 ± 2.25
Species mean		4.62 ± 0.54	2.30 ± 0.56	7.45 ± 0.85	5.86 ± 0.73	4.58 ± 0.60	5.78 ± 0.83	18.10 ± 1.67

TABLE 3. *TRICHOSTEMA* FLOWER MEASUREMENT RATIOS.

	Corolla tube			Stamens		
	Calyx	Upper lobe	Lip	Calyx	Corolla tube	Lip
T. ruygtii	1.38	2.27	1.79	1.67	1.20	2.16
T. lanceolatum	1.61	1.27	1.34	3.92	2.43	3.13

lanceolatum. Self-pollination is common in *Trichostema*. All of the California species have been found to be self-compatible and four of the eight annual species studied by Spira (1980) were deemed to be autogamous. The four autogamous species, *T. micranthum, T. austromontanum, T. oblongum, and T. simulatum*, have small flowers, with no measurable nectar and the stigma not exserted beyond the anthers. Potential pollinators were lacking in three and rare in one (*T. oblongum*). DNA studies by Huang (2002) indicate that two of the autogamous species, *T. oblongum* and *T. austromontanum*, are closely related. Her results together with the DNA study of Armstrong and Crawford (1960) tend to substantiate the suggestion of Lewis (1960) that *T. oblongum* is one of the diploid parental species of the allotetraploid *T. austromontanum*. However, none of these species shows the close relationship with an outcrossing species as *T. ruygtii* does to *T. lanceolatum*.

The DNA data of Huang (2002) indicate a very close relationship between *T. ruygtii* and *T. ovatum* (*T. ruygtii* was used to represent *T. lanceolatum* based on my identification of her material from Napa County in 1997; unfortunately, *T. lanceolatum* was not included in her studies). *Trichostema ovatum* is undoubtedly closely related to *T. lanceolatum* but differs most obviously in having smaller flowers and ovate rather than lanceolate leaves. According to Spira (1980) *T. ovatum*, like *T. lanceolatum*, has the stigma exserted beyond the anthers, nectar is produced, and flowers are visited by potential pollinators. However, of seven collections of *T. ovatum* locally available (LA), two have flowers for which the position of the stigma could be determined (Fresno Co. Mendota, *R. F. Hoover 2616*; Kern Co. Famoso, *R. F. Hoover 2674*). The stigma is not exserted beyond the anthers in either collection. Spira observed visits by three bee species during 14 hours of observation compared to seven species of bees observed to visit *T. lanceolatum* during a slightly longer period of time. Jake Ruygt observed visits to *T. ruygtii* by a species of skipper, a small native bee, a minute wasp or bee, and a bee fly. These visitors probably facilitate self-pollination and permit a small amount of outcrossing. Seed set was found by Spira to be about 93% for *T. ovatum*, comparable to that of autogamous species, including *T. ruygtii* and much higher than for *T. lanceolatum* (43.9%).

Trichostema ovatum occurs in a relatively small area in the southern San Joaquin Valley of California at elevations below 200 m. Like *T. ruygtii*, the area of distribution is distinct from that of *T. lanceolatum*, which is found in the surrounding area. *Trichostema ruygtii* and *T. lanceolatum* are not known to occur together; the closest known existing populations are separated by a distance of about 7.5 km. Ordinarily *T. ovatum* and *T. lanceolatum* are not found together but I once found a mixed population in a disturbed site along a road adjacent to cultivated fields at the northwestern margin of distribution of *T. ovatum*. Careful examination disclosed no hybrids. This led to the conclusion that the two taxa represent distinct species and not ecogeographic subspecies, as morphological similarities might suggest. Since *T. ruygtii* differs consistently from *T. lanceolatum* to a degree comparable to that of *T. ovatum* and no intermediates are known it seems desirable to recognize *T. ruygtii* as a species distinct from *T. lanceolatum*, a species from which both *T. ovatum* and *T. ruygtii* seem to have been derived.

I was curious as to how *Trichostema ruygtii* could have been misidentified as *T. rubisepalum* and why Mingjuan Huang went to look for *T. rubisepalum* in Napa County, far out of its known range. I found reasonable answers to both questions. Twenty years ago *A Flora of California* (Munz 1959) was in general use. An attempt to identify *T. ruygtii* using the key to *Trichostema* in that manual leads one to *T. rubisepalum* and the synoptic description of that species lists only traits that do not exclude *T. ruygtii*. Using the key in the current *Jepson Manual* (Hickman 1993) to try to identify *T. ruygtii* would probably lead to frustration rather than to the wrong species. However, in reading the description of *T. rubisepalum* in the *Jepson Manual*, I was startled to find that it is alleged to occur in Napa County! How this egregious error became inserted is hard to understand. I have been unable to locate any specimen in a major herbarium that purports to document what would be a very substantial extension of range of this rare species. As indicated above, Jake Ruygt has for many years been reporting new locations of "*T. rubisepalum*" in Napa County to the California Natural Diversity Database, providing a possible source of erroneous information. A note from Jake Ruygt assures me that my analysis and conclusion are correct.

Reports of a significant extension of range should not be included in any flora or checklist without documentation and verification.

KEY TO ANNUAL SPECIES OF *TRICHOSTEMA* IN CALIFORNIA

1. Petiole distinct, 5–15 mm long
   2. Corolla tube 4–8 mm long, exserted, lower lip 4–7 mm long. . . . . *T. laxum*
   2' Corolla tube 1.5–3 mm, included, lower lip 2–3 mm . . . .*T. simulatum*

1' Petiole indistinct or less than 5 mm long
   3. Corolla tube bent abruptly back as it narrows near the throat
      4. Stamens less than 10 mm long . . . . *T. ruygtii*
      4' Stamens 10–20 mm long
         5. Leaf blade lanceolate, 2–7 cm long, greater than 3 × width; corolla tube 5–10 mm long . . . . *T. lanceolatum*
         5' Leaf blade ovate, 1–2 cm long, less than 2 × width; corolla tube 2.5–5.5 mm long . . .*T. ovatum*
   3' Corolla tube curved gradually upward, not narrowed
      6. Hairs on stems and leaves curled or appressed; stamens 2–3 mm long, included or barely exserted . . . . *T. micranthum*
      6' At least some hairs on stems and leaves straight, spreading; stamens 3–6 mm long, exserted
         7. Calyx lobes less than 2 × tube; calyx tube longer than mature nutlets; mature calyx generally red-tinged . . . . *T. rubisepalum*
         7' Calyx lobes longer than 2 × tube; calyx tube shorter than mature nutlets; mature calyx green
            8. Leaf blade generally less than 4 × width; calyx lobes widest above base. . . . . . *T. oblongum*
            8' Leaf blade generally greater than 4 × width; calyx lobes widest at the base . . . . *T. austromontanum*

ACKNOWLEDGMENTS

I have recognized the extensive contributions of Jake Ruygt in naming the new species. I am also grateful to Arthur Gibson, Barry Prigge, Donald Lewis, Bruce Baldwin and Daniel Crawford for providing various resources and assistance. Special thanks go to Alan Smith for the Latin diagnosis and to Andria Ruygt for her illustration.

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CALAMAGROSTIS TACOMENSIS (POACEAE): A NEW SPECIES FROM WASHINGTON AND OREGON

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ABSTRACT

We used PCA of morphological characters to confirm the presence of an undescribed *Calamagrostis* species in Washington and Oregon that has historically been attributed to *Calamagrostis vaseyi*. We propose to name this grass *Calamagrostis tacomensis*. It is most similar to *C. foliosa* although it has often been confused with *C. purpurascens* and *C. sesquiflora* all of which have similar lemma awn characteristics (i.e., the awn relatively long, exserted, and bent). *Calamagrostis tacomensis* has been collected at high elevations (490–2170 m) in the Washington Cascades, the Olympic Peninsula and the Steens Mountains of Oregon. The name *C. vaseyi* has been misapplied to our new species. The description of *C. vaseyi* is similar to *C. rubescens*. We have studied the specimen that has been attributed to be the type of *C. vaseyi* and it is *C. purpurascens*. We lectotypify *C. vaseyi*.

Key Words: *Calamagrostis tacomensis*, *Calamagrostis vaseyi*, Poaceae, morphology, Washington, Oregon.

In preparing the treatment of *Calamagrostis* (Poaceae) for the Flora of North America, we noticed several specimens from the mountains of Washington and Oregon with long, exserted, and bent lemma awns that did not match descriptions of other northwestern North American species with similar awn characteristics such as: *C. sesquiflora* (Trin.) Kawano, *C. purpurascens* R. Br., *C. howellii* Vasey, and *C. foliosa* Kearney. Most such specimens had been identified initially, or annotated later as *C. sesquiflora*, but did not originate from habitats and geographic locations typical of *C. sesquiflora*, a plant of strictly maritime/coastal environments (Marr et al. in press). Some of these specimens had also been labelled at some point as "*C. vaseyi* Beal" leading us to reconsider the validity of this entity. We present morphometric data from herbarium specimens to support the recognition of this *Calamagrostis* entity (viz. "*C. vaseyi*") as a distinct species, and provide a botanical diagnosis, description and comparison to other related species. We propose the new name, *C. tacomensis* K. L. Marr & R. J. Hebda. We also designate a lectotype for *C. vaseyi* and show that the morphology of this specimen falls within the range of *C. purpurascens*.

MATERIALS AND METHODS

In our study, we included northwestern North American species whose floral morphology was similar to "*C. vaseyi*" in having long (greater than 4.5 mm), exserted, and bent lemma awns and often an open inflorescence (i.e., *C. purpurascens*, *C. sesquiflora*, *C. howellii*, and *C. foliosa*). Herbarium material (including five specimens of Russian *C. sesquiflora*) was borrowed from CAN, DAO, GH, JEPS, MO, NY, OSU, WTU, UBC, UC, US, and V, and collections at Olympic National Park and Pacific Lutheran University (Appendix 1). For 93 specimens, we measured or observed 20 leaf, inflorescence, and growth habit characters (Table 1). These data were used in the morphometric analyses and to develop species descriptions. In the descriptions, additional measurements were added in cases where those included in the morphometric analyses did not capture the full range of variation (e.g., leaf blade lengths and widths were based upon the widest, narrowest, longest, and shortest blades of the specimen regardless of position on the stem). For all specimens, we recorded information concerning habitat and collection locations.

To help establish whether or not the apparent entity is distinct from the taxa that it resembles, we applied principal components analysis (PCA) using SYSTAT (1997) in which we included the characters indicated in Table 1.

RESULTS

A non-statistical comparison of 21 characters suggests that several of them may be useful to distinguish among these species (Fig. 1). For example, *C. purpurascens* is the only species with densely tomentose upper leaf blade surfaces; inflorescence width of *C. howellii* (5.0–15.0 cm)

TABLE 1. CHARACTERS MEASURED ON SPECIMENS OF *CALAMAGROSTIS FOLIOSA*, *C. HOWELLII*, *C. PURPURASCENS*, *C. TACOMENSIS*, AND *C. SESQUIFLORA*. (+ designates characters used in PCA.)

Code	Explanation
Inflorescence	
+INFL	length (cm)
+INFW	width at widest point, usually the inflorescence base (cm)
+BRL	longest branch from the most basal inflorescence node (mm)
Spikelet	
+GL	first glume length (mm)
+LML	lemma length (mm)
GVERSUSL	glume length minus lemma length
+GSR	glume surface: 1 = glabrous; 2 = scabrous on keels only; 3 = whole surface scabrous; 4 = scabrous and projections longer and bent
HRAT	callus hair length/lemma length
AWBSRAT	distance from base of lemma to point of attachment of awn/lemma length
+AWNATT	distance from base of lemma to point of attachment of awn
+AWNL	awn length (mm)
Leaf	
+LFW	width of second leaf below inflorescence (mm)
+LFL	length of second leaf below inflorescence (mm)
+INV	leaf blade: 1 = involute; 2 = flat
+ULFS	upper leaf surface: 1 = glabrous; 2 = slightly scabrous; 3 = very scabrous; 4 = scabrous + slightly pilose; 5 = tomentose
+LLFS	lower leaf surface: 1 = glabrous; 2 = scabrous
+COLLAR	collar: 1 = glabrous; 2 = scabrous; 3 = pilose; 4 = tomentose
+LIGL	ligule length (mm)
Stem	
+HT	total plant height (cm)
+NODE	number of nodes (from the root crown to the inflorescence)

is greater than that of the other species (0.5–3.0 cm); awns of *C. foliosa* (12.0–17.0 mm) and *C. howellii* (10.0–16.0 mm) are generally longer than those in the other three species (4.5–13.0 mm). Based on this comparison, *C. tacomensis* is most similar to *C. foliosa*, differing mostly from the latter in having shorter awns, glumes, lemmas, and callus hairs. Although it was not part of our analysis, *C. tacomensis* also occurs at much higher, inland sites than *C. foliosa*.

In the first PCA, the first factor accounted for 31% of the variation with awn length (AWNL), upper leaf surface (ULFS), and longest inflorescence branch (BRL) contributing most to the variation (see Table 1 for details). The second factor accounted for 16% of the variation with plant height (HT), lower leaf surface (LLFS), and number of nodes (NODE) contributing the most. A scatterplot (Fig. 2) of the PCA scores indicated that *C. purpurascens* and *C. sesquiflora* were morphometrically distinct. There was more overlap among *C. foliosa*, *C. howellii*, and *C. tacomensis*, nevertheless most specimens of *C. tacomensis* were visibly distinct from the other species. Three of the *C. sesquiflora* specimens from Russia clustered together with those from North America; the other two did not. The scatterplots confirmed Scribner's (1901) statement to the effect that *C. tacomensis* (his *C. vaseyi* Beal, see below) is morphologically intermediate between *C. purpurascens* and C. *howellii*. The specimen (US-556750) that we have designated as the lectotype of *C. vaseyi* plotted well outside of the range for *C. tacomensis* and clearly together with *C. purpurascens*.

In a second PCA, we removed *C. purpurascens* and *C. sesquiflora* from the analysis and included the same set of characters as the first PCA. The first factor accounted for 29% of the variation with lemma length (LML), callus hair length (HARL) and glume length (GL) contributing the most. The second factor accounted for 18% of the variation with plant height (HT), leaf width (LFW) and inflorescence length (INFL) contributing the most. The third factor accounted for 12% of the variation with inflorescence width (INFW), upper leaf surface (ULFS), and inflorescence branch length (BRL) contributing the most. A scatterplot (Fig. 3) of the PCA scores indicated that there was almost no overlap among *C. foliosa*, *C. howellii*, and *C. tacomensis*, especially on the first axis.

DISCUSSION

Our analyses indicate that there is a group of specimens that are morphologically as well as ecologically and geographically distinct from any of the currently recognized species of *Calamagrostis*. Earlier botanists noted that these

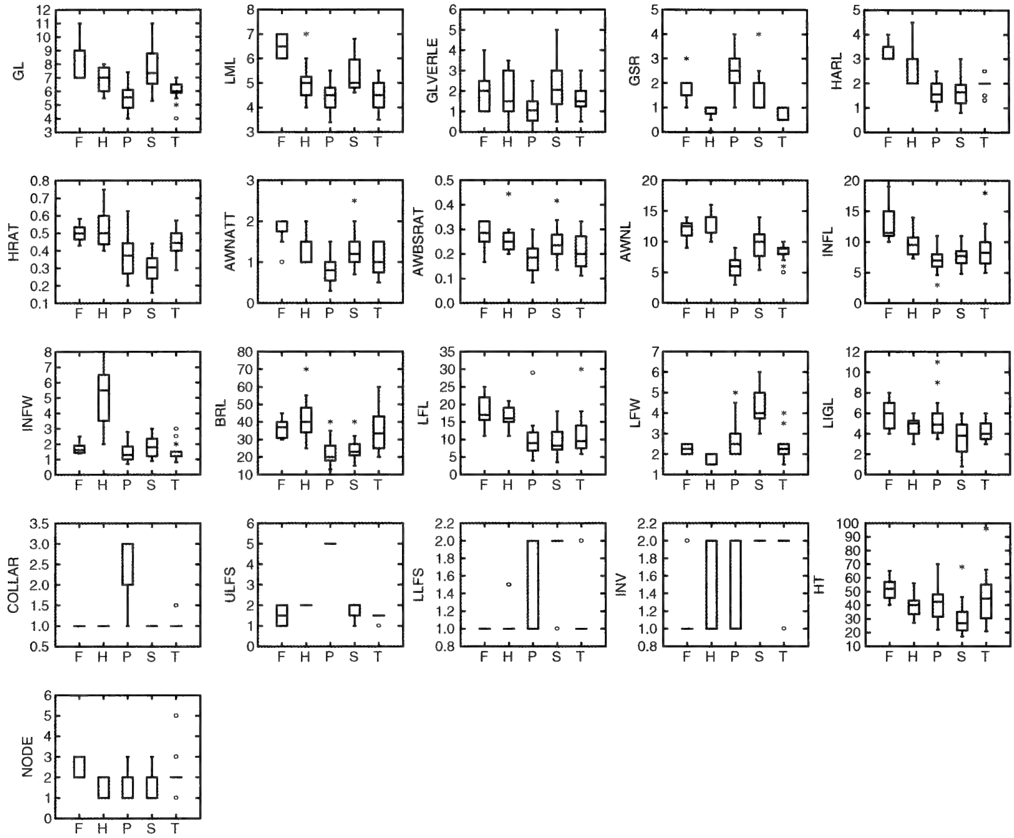

FIG. 1. Univariate plots of characters measured for *Calamagrostis* species from northwestern North Amercia having long, exserted, and bent awns. Species labelled as following: F = *C. foliosa*, H = *C. howellii*, P = *C. purpurascens*, S= *C. sesquiflora*, T = *C. tacomensis*. All length measurements in millimeters, except for the following that are in centimeters: INFL, INFW, LFL, and HT. Character abbreviations per Table 1.

plants are distinct from other species of *Calamagrostis*, and sometimes misapplied the name "*C. vaseyi*" to them. Furthermore, the specimen that has been regarded as the type of *C. vaseyi* belongs to *C. purpurascens*. In the following section we outline the history of *C. vaseyi* and demonstrate why the name cannot be used. We provide a name, *C. tacomensis*, for the above mentioned group of specimens and a key and descriptions for *C. tacomensis* and morphologically similar species of northwest North America.

Taxonomic and Nomenclatural History of *Calamagrostis vaseyi*

Calamagrostis vaseyi Beal was first published in Beal (1896). The protologue indicates that it was based on a collection made by U.S. Department of Agriculture botanist, G. R. Vasey: "Washington (Cascade Mountains), *Vasey*. Alaska to Washington." In the US type collection there is a specimen (US-556750), that has been considered the type specimens for *C. vaseyi* (Fig. 4). This specimen has been annotated by at least three different individuals, none of whom gave their name. Beal was not one of them. One annotation is simply "Type of *C. vaseyi* Beal." In the handwriting of a second person are the following two statements: 1) "In Beal Herb. is a duplicate of this with labels in Vasey's script "Calamagrostis purpurascens R.Br.—the genuine plant"; and 2) "It is not named "*C. vaseyi*"—there is no Beal script in connection with this specimen". Following the first statement above, lightly in pencil is written "cf. *C. purpurascens.*" In the handwriting of a third person are the following: "*Calamagrostis rubescens* ["*rubescens*" has been crossed out]; locality: Cascade Mts. Washington; collector G.R. Vasey 1889." Hitchcock et al. (1969) noted, and we agree, that this specimen is actually *C. purpurascens.* Beal (1896) designated a type collection for *C. vaseyi* but did not specify a particular sheet in a specific herbarium. To preclude future nomenclatural problems, we are designating US-556750 as the lectotype of *C. vaseyi*, a designation that is in keeping with past practice. We have been unable to locate the specimen that is alluded to in comment 1 above.

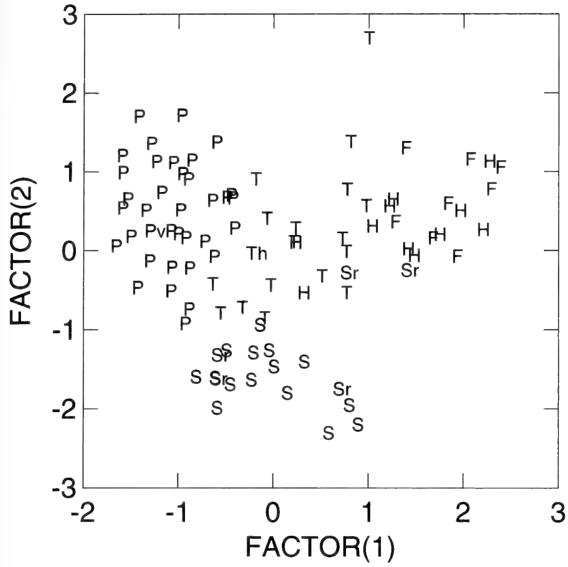

FIG. 2. Scatterplot of the first two components from a PCA of morphological characters of northwest North American *Calamagrostis* species having long, exserted, and bent awns. Species labelled as following: F = *C. foliosa*, H = *C. howellii*, P = *C. purpurascens*, S = *C. sesquiflora*, Sr = *C. sesquiflora* collected from Russia, T = *C. tacomensis*, Pv = *C. vaseyi* lectotype, Th = *C. tacomensis* holotype.

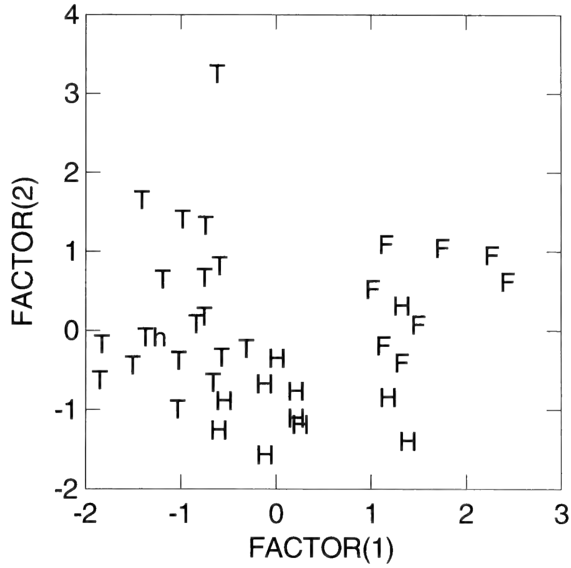

FIG. 3. Scatterplot of the first two components from a PCA of morphological characters of selected northwest North American *Calamagrostis* species having long, exserted, and bent awns. Species labelled as following: F = *C. foliosa*, H = *C. howellii*, T = *C. tacomensis*, Th = *C. tacomensis* holotype.

Calamagrostis vaseyi Beal—LECTOTYPE HERE DESIGNATED: U.S.A: "Cascade Mts. Washington", 1889 *G.R. Vasey s.n.* (Lectotype: US 556750).

Beal's description for *C. vaseyi* matches that of *C. rubescens* Buckley in the following characters: leaf length and width, the presence of hairs at the leaf collar, glume length, awn length and position of attachment to the lemma, and callus hair length. He described the awn as straight, whereas it is bent in *C. rubescens*. Scribner (1901) recognized *C. vaseyi* Beal, and provided an illustration in his own hand (we do not know what specimens he viewed) and noted that *C. vaseyi* is "intermediate between *C. purpurascens* and C. *howellii*." However, neither Scribner's description, nor his illustration, matches the description given by Beal (1896). Under synonymy, Scribner stated: "*C. purpurascens* of Vasey, Contr. U.S. Nat. Herb. 3:82, 1892. Not R. Br. 1823." Vasey (1892), under *C. purpurascens* states the following: "This description is from specimens collected in the Cascade Mountains of Washington by G. R. Vasey, which agrees well with European specimens, although differing somewhat from the description in Hooker's Fl. Bri. Am. It occurs also in British America and in Sitka." From these comments it is evident that Vasey perceived that the entity he collected in 1889, and described as *C. purpurascens*, did not entirely match *C. purpurascens* R. Br.

Calamagrostis vaseyi was recognized as distinct from *C. purpurascens* in several early regional floras of British Columbia (Henry 1915) and the Pacific Northwest (Howell 1897; Piper 1906; Frye and Rigg 1912; Abrams 1923; Jones 1938). The descriptions by these authors differ somewhat from each other and most seem to fit *C. purpurascens*. Only Piper (1906) cites specimens he actually viewed, from the following locations: Olympic Mountains, Mount Rainier, Goat Mountains, and Skamania County. Piper and Beattie (1915) listed *C. vaseyi* but not *C. purpurascens*. Hitchcock (1951) listed *C. vaseyi* under *C. purpurascens*.

Calamagrostis vaseyi has also been confused with *C. sesquiflora*. Kawano (1965) in his treatment of the "*C. purpurascens* complex" viewed ten Washington state specimens and concluded that they belonged to *C. sesquiflora*. It appears that this was the first application of the name *C. sesquiflora* to plants from Washington State. Hitchcock et al. (1969) followed Kawano (1965) and reported that *C. sesquiflora* occurred "On cliffs and shaded to open rocky montane to subalpine slopes in our area, mostly at elevations of 3500–6000 ft.; Olympic Mts., and the Cascade and Wenatchee Mts., Wash., from Kittitas Co. to Skamania Co.; Aleutian Is. to n.e. Asia."

We have viewed most of the specimens from Washington that Kawano annotated as *C. sesquiflora*; all fit the concept and criteria of

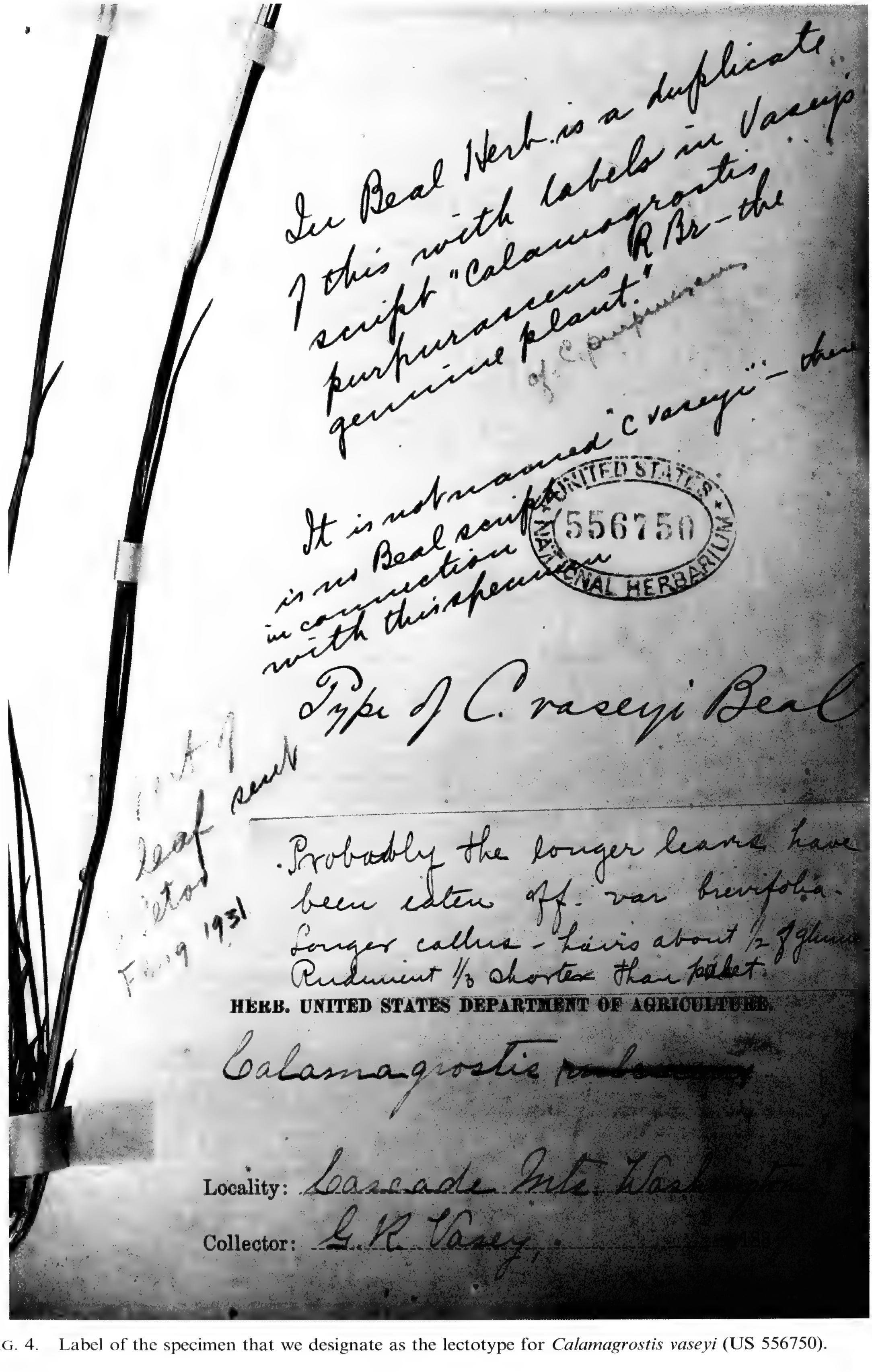

FIG. 4. Label of the specimen that we designate as the lectotype for *Calamagrostis vaseyi* (US 556750).

what we propose to call *C. tacomensis* (Fig. 5), a previously overlooked species that is distinct from both *C. purpurascens* and *C. sesquiflora* (Figs. 2, 3). These specimens bore earlier labels identifying them as either *Trisetum sesquiflorum* Trin., *Deyeuxia sylvatica* Kunth var. *americana* Vasey, *C. purpurascens* R. Br. or *C. vaseyi* Beal. Further confusion resulted because some specimens that are actually *Trisetum spicatum* (L.) Richt., have been annotated as *Calamagrostis sesquiflora* arising from the earlier inclusion of the species in *Trisetum*.

Typification of *Calamagrostis tacomensis*

"Tacoma" is a Native American name for Mt. Rainier near Seattle; because many collections of this species come from that mountain, we chose it for the specific epithet. To our knowledge, the specimen that we have chosen for the type is the earliest collection made.

Calamagrostis tacomensis K. L. Marr and R. J. Hebda, sp. nov.—TYPE: U.S.A. Washington: Skamania County, rocky mountain-sides, 11 Aug. 1886, *W.N. Suksdorf 909* (Haplotype: MO-1772987!; Isotype: NY!)

A *Calamagrostis foliosa similaris*, sed glumis, lemmae, aristae et pilis calli brevioribus.

Plants without sterile culms; cespitose, sometimes densely so, usually without rhizomes, if present, rhizomes short (about 2 cm) and stout (2–3 mm thick). Culms (20)30–55(95) cm, unbranched, smooth or slightly scabrous beneath the panicles; nodes (1)2(5). Sheaths and collars smooth to slightly scabrous; ligules (3)3.5–5.5 (6) mm, mostly entire and truncate to obtuse, sometimes lacerate; blades (6)7–14(30) cm long, (1.5)2–2.5(4) mm wide, flat, abaxial surface smooth or rarely slightly scabrous, adaxial surface usually slightly scabrous, rarely smooth. Panicles (5)7–10(18) cm long, (0.5)1–2(3) cm wide, loosely contracted, sometimes open, erect to slightly nodding, shiny green and purple; branches (2)2.3–4(6) cm long, scabrous, with spikelets mostly on the distal 2/3, sometimes to the base. Spikelets (4)6–6.5(7) mm, often green with a purple patch at the base; rachilla prolongations 1.5–2(2.5) mm, with (1.5)2(3) mm hairs. Glumes keeled, sparsely scabrous on the keel towards the glume apices, lateral veins mostly prominent, apices acute to short acuminate, tips not twisted; callus hairs (1.2)2(2.5) mm, (0.3)0.4–0.5(0.6) times as long as the lemmas, abundant; lemmas (3.5)4–5(5.5) mm, (0.5)1.5–2(3) mm shorter than the glumes; awns (5.5)7–8.5(10) mm, attached to the lower 1/10–1/3 of the lemmas, exserted (greater than 2 mm), easily distinguished from the callus hairs, strongly bent; anthers (1)2–3(3.5) mm. 2n = unknown.

FIG. 5. Illustration of *C. tacomensis*.

Comments. The type specimen of *C. tacomensis* was originally labelled as *Deyeuxia sylvatica,* Kunth, var. (*Deyeuxia* is a genus sometimes combined with *Calamagrostis.*) The holotype has been annotated as *C. vaseyi* Beal. At US is a third specimen that we have seen whose label bears the following: "*Deyeuxia.* Dry rocks on high mountains 11 Aug. 1886, *Suksdorf 201.*" The epithet *sylvatica* was added later in a different handwriting; a third person later annotated it as *C. vaseyi* Beal. Because the US specimen bears a different collection number, we have not included it as an isotype, although it was evidently collected from the same location and on the same date.

Calamagrostis tacomensis is currently known only from three regions: Cascade Mountains of Washington, the Olympic Peninsula of Washington, and the Steens Mountains of southeast Oregon. The Steens Mountains specimens are somewhat more robust than those of Washington State. Clarification of the taxonomy of this and the other morphologically similar species removes *C. sesquiflora* from the flora of Washington State.

Ecology of *Calamagrostis tacomensis*

Calamagrostis tacomensis grows in mountains, mostly in open, moist to dry sites from 490–2170 m. Notable on many of the herbarium labels are the words "rock", "rocky", "crags" and "cliffs", but sandy and sandy loam soil textures are also recorded, and the species occurs from ridge top to valley bottom positions.

Compared to morphologically similar species in the region, the ecological requirements seem to be similar to but probably macroclimatically moister and milder than those of *C. purpurascens,* a species that also occupies mid to high elevations but is mostly in more continental climates. Unlike *C. tacomensis, C. purpurascens* is commonly associated with forested conditions in addition to the open habitats typical of *C. tacomensis.* Compared to *C. sesquiflora*, the relative macroclimatic conditions of *C. tacomensis* are more inland and continental. *Calamagrostis sesquiflora* would seem in North America at least to have limited drought and cold tolerance, growing predominantly in sites within a few kilometres of the open ocean or at sites under strong maritime influence from sea-level to 1100 m. Although it occurs on rocky sites, these are almost always moist and soils with abundant organic matter (bogs, heaths) are often noted.

Like *Calamagrostis tacomensis, C. foliosa* and *C. howellii* have a limited geographic distribution and a preference for rocky sites and cliffs. Both, however, are lower elevation species (*C. foliosa* from 0–1220 m and *C. howellii* from 100–450 m) suggesting limited or no tolerance of significant frost, particularly *C. foliosa.* Of all the morphologically similar species, *C. howellii* grows in the most similar habitats and nearest to *C. tacomensis*, but at lower elevations and for that reason likely under drier conditions.

Conclusions

It is critical to carry out comprehensive field surveys, collections, and ecological/habitat observations of *C. tacomensis*, because it appears to have a limited distribution. The range may well be greater than so far recognized by us from herbarium material. A thorough investigation of the southern Cascade Mountains northward into British Columbia and the Olympic Mountains is required as well as isolated adjacent high ground. In this context, the morphological distinctness of *C. tacomensis* in the Steens Mountains suggests either long-distance dispersal or more likely relict populations of a species that was more widespread during cool climates of the late Pleistocene. A genetic study using DNA markers might clarify the above question as well as evaluate the relationship of *C. tacomensis* to the other long-awned species of this region, in particular *C. foliosa.* It would also be useful to have a chromosome count for this species.

Key to some Long-Awned *Calamagrostis* Species from British Columbia, Washington, Oregon and California

1a. Blades densely hairy on the adaxial surfaces; awns 4.5–9 mm.. . . . . *C. purpurascens*
1b. Blades glabrous, scabrous or sparsely hairy on the adaxial surfaces; awns 5–17 mm.. 2
  2a. Panicles open, (2)3.5–6.5(8) cm wide when pressed, branches usually with spikelets confined to the distal 1/2 of the branches; awns 10–16 mm long . . . . *C. howellii*
  2b. Panicles usually contracted, 1–3 cm wide when pressed or, if open, the branches usually bearing spikelets-to the base; awns 5–17 mm long. 3
    3a. Awns 12–14(17) mm long; plants of California. . . . . *C. foliosa*
    3b. Awns (5.4)7–11(13) mm long; plants of Alaska , British Columbia, Washington, and Oregon. 4
      4a. Glume apices long-acuminate and usually twisted at the tips; glume keels scabrous for most of their length . . . . *C. sesquiflora*
      4b. Glume apices usually acute, if acuminate, the tips not twisted; glume keels smooth or scabrous only on the distal 1/2. . . . . *C. tacomensis*

Calamagrostis foliosa. Plants sometimes with sterile culms; cespitose, short (less than 1 cm) rhizomes rarely present. Culms (25)30–60(70) cm, unbranched, sparsely scabrous beneath the panicles; nodes 1–3. Sheaths and collars usually smooth; ligules (3)4–6(7) mm, mostly entire and truncate to obtuse, sometimes lacerate; blades (10)11–21(27) cm long, (1.5)2–2.5(4) mm wide, mostly basal, flat or involute, abaxial surface smooth, adaxial surface slightly scabrous. Panicles (9)10–12(19) cm long, 1–1.5(2.5) cm wide, erect to slightly nodding, contracted, branches sometimes slightly spreading at the base, usually pale green, rarely pale purple; branches (2)3–4(5) cm, sparsely scabrous, with spikelets to the base. Spikelets (7)8–11 mm; rachilla prolongations (1.5)2–(3) mm, prominently bearded, hairs to 2–3 mm. Glumes keeled, smooth or scabrous on the keel, lateral veins prominent, apices acuminate; callus hairs 2.5–3(4) mm, 0.4–0.6 times as long as the lemmas, abundant; lemmas (5)6–7(8) mm, (0.5)1–2(3) mm shorter than the glumes; awns 12–14(17) mm, attached to the lower 1/5–2/5 of the lemmas, exserted (greater than 2 mm), easily distinguished from the callus hairs, bent; anthers 3–4.5 mm. 2n = 28.

Calamagrostis howellii. Plants sometimes with sterile culms; densely cespitose, rhizomes rare, if present, less than 1 cm. Culms (25)35–45(60) cm, unbranched, smooth or slightly scabrous beneath the panicles; nodes 1–2. Sheaths and collars smooth; ligules (2.5)3.5–6 mm, lacerate, if not too torn then acute; blades (9)12–20(25) cm long, 1–2.5(3) mm wide, flat to involute, abaxial surface smooth, adaxial surface finely scabrous. Panicles (5)7–12(15) cm long, (2)3.5–6.5(8) cm wide, loose and open, straw-colored, green to purplish; branches (2)3.5–5(7) cm, smooth or sparsely scabrous, with spikelets often, but not always, concentrated in the distal 1/2 of the branchlets. Spikelets (5.5)6–8 mm; rachilla prolongations 1–1.5(2) mm, with (1.5)2–2.5(3) mm hairs. Glumes rounded to slightly keeled, smooth or scabrous only on the apices, lateral veins usually prominent and raised, apices acuminate; callus hairs 2–3(4.5) mm, 0.4–0.6(0.7) times as long as the lemmas, abundant; lemmas 4.5–5 mm, about 2 mm shorter than the glumes; awns (10)13–16 mm, attached to the lower 1/5–2/5 of the lemmas, exserted, stout, easily distinguished from the callus hairs, strongly bent; anthers (2)2.5–3(4) mm. 2n = 28.

Calamagrostis purpurascens. Plants apparently without sterile culms; strongly cespitose, often with short (1–4 cm), moderately stout (1–2 mm thick) rhizomes. Culms (10)30–80 cm, usually unbranched, occasionally branched, slightly to strongly scabrous, sometimes short hairy beneath the panicles; nodes (1)2(3). Sheaths scabrous; collars mostly scabrous to hairy, rarely smooth; ligules (1.5)2–4(9) mm, usually entire and truncate, sometimes lacerate. Blades (4)5–17(30) cm long, 2–5(6) mm wide, flat or involute, stiff, abaxial surfaces scabrous, adaxial surfaces densely long hairy, rarely sparsely hairy. Panicles 4–13(15) cm long, 0.9–2(2.8) cm wide, erect, contracted, infrequently interrupted near the base, often red- or purple-tinged; branches 1.3–3.5 cm, scabrous, with the projections long, almost hairy, and with spikelets to the base. Spikelets (4.5)5.5–6.5(8) mm, with 1(2) florets; rachilla prolongations about (1)2 mm, with about 2 mm hairs. Glumes keeled, commonly scabrous on the entire surface, rarely scabrous on the keel only, lateral veins obscure to prominent, apices acute; callus hairs (0.9)1.2–1.5(2.4) mm, 0.2–0.4(0.6) times as long as the lemmas, sparse; lemmas (3.5)4–4.5(5) mm, 1–2.5 mm shorter than (rarely equal to) the glumes; awns (4.5)6–7(9) mm, attached to the lower 1/10–1/3 of the lemmas, exserted (except rarely when the awn is 4.5–5 mm long), stout, easily distinguished from the callus hairs, bent; anthers (1.3)1.7–2.5(2.9) mm. 2n = 42–58, 84.

Calamagrostis sesquiflora. Plants rarely with sterile culms; strongly cespitose, usually without rhizomes or with short (1–2 cm), moderately stout (1–2 mm thick) rhizomes. Culms (15)30–46(50) cm, unbranched, usually smooth, rarely slightly scabrous beneath the panicles; nodes 1–2(3). Sheaths and collars smooth; ligules (0.5)2–5(6) mm, entire and mostly truncate (obtuse) to lacerate; blades (3)8–25(31) cm long, (2)3–7 mm wide, flat, abaxial surface scabrous, rarely smooth, adaxial surface smooth or slightly scabrous. Panicles 4–11(12) cm long, 0.8–2.5(2.8) cm wide, erect, contracted to somewhat open, usually purple-tinged, sometimes brown or green; branches 1.5–3(4) cm, scabrous, with the projections sometimes long, almost hairy, and with spikelets to the base, except sometimes on the lowest branches. Spikelets (5)5.5–8.5(9.5) mm; rachilla prolongations (1)1.5(2.2) mm, with 1–2.2 mm hairs. Glumes keeled, scabrous, usually for the full length of the keel and sometimes on the entire surface, lateral veins prominent, apices long-acuminate, tips often twisted; callus hairs (0.8)1.2–1.8(3) mm, 0.1–0.4 times as long as the lemmas, abundant; lemmas (3.5)4–4.5(6) mm, (0.5)1–2.5(4.5) mm shorter than the glumes; awns (5.4)7–11(13) mm, attached to the lower 1/10–2/5 of the lemmas, exserted (greater than 2 mm), stout and easily distinguished from the callus hairs, bent; anthers (1.2)2.2–3(3.4) mm. 2n = 28.

Acknowledgments

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Gandhi provided important advice on nomenclatural issues. Mary Barkworth offered many useful suggestions to improve this paper. Thanks to Kim Martin for photographing the lectotype of *C. vaseyi* and Hana Pazdirkova for the illustration of *C. tacomensis*. We appreciate two anonymous reviewers who contributed substantially to improving this paper.

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Appendix I

Specimens Examined

* = specimen included in morphometric study;

(Herbarium abbreviations are according to acronym except for the following: Luth. = Pacific Lutheran University; Olym = Olympic National Park Herbarium)

Calamagrostis foliosa: USA, **California: Del Norte Co.:** Red Mountain, E of Klamath Glen; Six Rivers National forest, 4000 ft, 7 July 1964, *Van Deventer 1054-B*, (JEPS); **Humboldt Co.:** Hardy Creek, May-1900, *Joseph Burtt Dav, 6602* (UC); Mattole river at bridge 3 miles E of Petrolia, 100 ft, 9 June 1936, *Tracy 14899** (OSU,UC); near "Panther Gap" on road between Mattole and Bull Creek, 2700 ft, 17 June 1938, *Tracy 15967A*,15967B** (UC), 145052; Shelter Cove, mouth of Telegraph Creek, 13-Sep-1986, *Berg s.n.* (UC); mouth of Hardy Creek, May 1900, *Davy, s.n.**, (GH); **Mendocino Co.:** 31 July 02, *Congdon s.n.** (GH); Bridal Veil, 24 June 1911, *Peck 994* (OSU); Hoerlein's, along Hood River, 45°43′N, 121°32′W, 14 June 1924, *Henderson 1023* (GH, OSU); Oneanta tunnel, Columbia River Gorge, 12 June 1928, *Thompson, 4705*, (WTU); *Calamagrostis howellii*: USA, **Oregon: Multnomah Co.:** John Yeon State Park, by McCord Creek, along Columbia R. Highway, 28-Sep-1980, *Chambers 4746* (OSU); Lataurelle Falls, 3 July 1935, *Thompson, 11842*, (WTU); Multnomah Falls, 2 July 1965, *Hitchcock 23746* (WTU); McCord Cr., near Warrendale, Columbia River Gorge, May-1972, *Jaques s.n.* (OSU); Columbia R. gorge, on Tanner Creek, near the falls 1 miles. of Hwy. 80N; R7E, T2N, NE1/4 of Sect. 33, 320 ft., 29 Aug. 1976, *Kemp, s.n.** (OSU); **Hood River Co.:** Canyon of Eagle Cr., 30 May 1927, *Peck 14924** (OSU); at Latourell falls, 2 July 1965, *Hitchcock 23740** (OSU); Multnomah Falls, 14 Jun 1903 *Sheldon S.12110* (OSU); Cliffs of Columbia River near the Cascades, May 1881, *Howell s.n.* (WTU); Hood R., May 1891 (OSU); Sandy R., 9 July 1883, *Henderson s.n.* (OSU); Rooster Rock, July 1889, *Gorman s.n.* (WTU); **Washington: Skamania Co.:** Cooks, 45°43′N, 121°40′W, 9 July 1909, *Suksdorf s.n.* (GH); Cooks, 9 July 1909, *Suksdorf s.n.** (WTU); along the Columbia R. in drier areas of cliffs at Cape Horn; at e. end of railroad tunnel, 8 July 1966, *R.&M. Spellenberg & Sutherland 1189** (OSU,WTU,UBC); Prindle, 26 May 1924, *Suksdorf 11696* (WTU).

Calamagrostis purpurascens: CANADA, **British Columbia**, Cheslatta, Cariboo-Chilcotin, Kritchlow property; 1 kilometre E of Cheslatta, 53°48′36″N, 125°47′12″W, 12 July 01, *Hebda & Fitton 01-19119**, (V); Robb Lake, Peace River, slopes on N side of lake, 56°54′N, 123°48′W, 1524 m, 30 July 1977, *Argus & Haber, 10303** (V); Fern Lake, Peace River, near and around outlet E end of the lake, 57°45′N, 124°47′W, 1371.6 m, 5 Aug. 1977, *Argus & Haber 10642** (V); Wokkpash Lake, Liard River Basin, slopes-W of the NW end of the lake; S of the creek, 58°27′N, 124°53′W, 1280.16 m, 19 July 1977, *Argus & Haber 10729** (V); Gladys Lake, Stikine River, SE face of Ptarmigan Ridge, 57°35′N, 128°47′W, 1280 m, 16 July 1975, *Pojar 107f** (V); Mt. Stephen, Yoho National Park, at Field, 49°50′N, 115°34′W, 2133 m, 19 Aug. 1953, *Calder & Savile 12070** (DAO); Pope, Mount, Cariboo, a few miles NW of Fort St. James, 54°30′N, 124°20′W, 1472 m, 31 July 1954, *Calder, Savile & Ferguson 13817** (V); Flathead area; Inverted Ridge, Kootenay, S Peak and saddle N of it, 49°07′N, 114°45′W, 31 July 1983, *Ogilvie & Ceska, 15902** (V); Begbie, Mount, Cariboo,

51°29′N, 121°22′W, 23 June 1944, *Eastham 17026** (V); Sinkut Mountain, Cariboo-Chilcotin, near Vanderhoof, 53°49′N, 123°58′W, 1463m, 18 July 1945, *Eastham 18828**, (V); Skagit River, Lower Fraser Valley, Unnamed mountain 2217 m total height S of Finlayson Peak in Skagit Drainage, 49°05′N, 121°13′05″W, 2150 m, 12 Aug. 1988, *Ceska,& Ogilvie 24997** (V); Skookumchuck, Kootenay, 0.1 mile up Regional Garbage Dump Road, 49°44′N, 115°43′W, 750 m, 2 July 1976, *Ferster 76-1978** (V); Taseko River, Cariboo-Chilcotin, valley side on E by Taseko River Road, 51°36′N, 123°42′W, 1370 m, 14 July 1978, *Pavlick & Sax 78-19571** (V); Tanzilla River, 2 kilometres above junction with Stikine River, 58°03′N, 130°54′W, 650 m, 10 July 1980, A.&O. *Ceska & Polster 8054** (V); Hutchison Lake, 59°47′30″N, 126°40′W, 760 m, 21 Aug. 1979, A.&O. *Ceska, Polster, & Martens 8061** (V); Buckley Creek, above Klastline River, 58°56′N, 130°46′W, 600 m, 29 Aug. 1979, A.&O. *Ceska & Polster 8073** (V); Upper Dean River Road, 52°33′N, 125°19′30″W, 1100 m, *Harcombe AH-1979-1930** (V); Flathead, Kootenay, ca. 5 mi. from Canada-US border, 49°08′N, 114°35′W, 2042 m, Jul-1973, *Dick FR24** (V); Liard Hot Springs Park, Liard River, 59°25′N, 126°06′W, 430 m, 10 July 1971, *Brayshaw & Barrett s. n.** (V); Mount Ole, Liard River, Liard Hot Springs Provincial Park, 59°25′N, 126°03′W, 760 m, 7 July 1971, *Brayshaw & Barrett s. n.** (V); Tuya River, Stikine District, breaks of the river, 5 miles above crossing, 58°08′N, 130°44′W, 610 m, 8 Aug. 1971, *Brayshaw & Barrett s.n.** (V); Lillooet, Headwaters of Blue Creek, 51°02′N, 122°28′W, 1430 m, 13 July 1987, *Ceska, Ceska, Britton, & Anderson s.n.** (V); Cassiar, Cassiar District, 59°15′N, 129°45′W, 1000 m, 18 June 1956, *Taylor, Szczawinski & Bell 391** (V); Telegraph Creek, Stikine River, slopes above Day's Ranch, 58°02′N, 130°53′W, 10 June 1980, A.&O. *Ceska & Polster 4070** (V); Lower Porcupine Valley, Kootenay, Yoho National Park, 51°30′ N, 116°30′W, 1250 m, 11 Aug. 1974, *Kuchar 4077** (V); **Alberta**, Mt. Edith Cavell, Jasper National Park, 52°40′N, 118°03′W, 28 Aug. 1964, *Calder, J. A, 37200**, (DAO); Lake Edith, Jasper National Park, YMCA Lodge, 52°55′N, 118°02′W, 4 July 1955, *Jenkins 5817** (DAO); **Ontario**, Thunder Bay, Sibley Peninsula, Thunder Cape, at the knees of Sleeping Giant, 48°18′N, 085°60′W, 24 Aug. 1957, *Garton 4398** (V); **Yukon** Haines Junction, Kluane National Park, 4 miles E of the junction of Kawkawulsh and Dezadeash Rivers; ca. 8 miles WSW of the Junction, 60°45′N, 137°30′W, 610 m, 1 Aug. 1973, *Douglas & Douglas 6704** (V). USA, **Alaska:** Talkeetna Mountains, 62°48′N, 148°01′W, 850 m, 2-Sep-1978, *Talbot T8023-V-1915** (DAO); **Washington: Jefferson Co.:** Buckhorn Mountain, Olympic National Park, T27N R4W S13 SE1/4, 47°49′N, 123°06′W, 2130 m, 8 June 1979, *Buckingham 2129**, (OLYM); Royal Basin, Olympic National Park, Ridge between Royal Creek and Dungeness River, 48°08′N, 123°07′W, Aug.-1983, *Dalton 2656** (OLYM); **? Co.:** Cascade Mts. *Vasey s.n.**, (US 556750).

Calamagrostis sesquiflora: CANADA, **British Columbia**, QCI, 53°10′N, 132°27′W, 24 July 1897, *Newcombe 18699* (CAN); Athlow Bay, QCI, 53°38′N, 132°59′W, 122 m, 13 June 1957, *Calder & Saville 21456* (DAO); McCliton Cr., QCI, 53°39′N, 132°35′W, 19 June 1957, *Calder, Taylor & Saville, 21662* (DAO); Skidegate Channel, QCI, 53°09′N, 132°31′W, 91 m, 25 July 1957, *Calder, J. A.; Taylor, R. L.; Saville, D. B. O., 22928*, (DAO); Newton Point, QCI, 53°08′N, 132°30′W, 25 July 1957, *Calder, Taylor & Saville 22966* (DAO); Moresby Logging Camp, QCI, 52°55′N, 132°03′W, 29 July 1957, *Calder, Taylor & Saville 23126* (DAO); Shields Bay, QCI, 53°21′N, 132°29′W, 731 m, 8 Aug. 1957, *Calder & Taylor 23279* (DAO); Jalun Lake, QCI, 53°58′N, 132°52′W, 625 m, 1 July 1964, *Calder, J. A.*; *Taylor, R. L., 35644*, (DAO); Long Arm, QCI, 53°12′N, 132°16′W, 305 m, 15 July 1964, *Calder & Taylor 35976* (DAO); Kootenay Inlet, QCI, 52°51′N, 132°11′W, 21 July 1964, *Calder, J. A.*; *Taylor, R. L., 36192*, (DAO); QCI, 52°56′N, 132°04′W, 570 m, 25 July 1964, *Calder & Taylor 36310* (DAO); Sunday Inlet, QCI, 52°39′N, 131°55′W, 2 m, 5 Aug. 1964, *Calder & Taylor 36639* (DAO); QCI, 23 July 1910, *Spreadborough, 87609*, (CAN); Bigsby Inlet, QCI, 52°37′N, 131°45′W, 213 m, 5 July 1957, *Calder, Taylor & Saville, 22141** (DAO); Graham Island, QCI, 53°20′N, 132°25′W, 732 m, 8 Aug. 1957, *Calder & Taylor 23279** (V); Mt. de la Touche, QCI, 52°42′N, 132°02′W, 610 m, 16 Aug. 1957, *Calder & Taylor 23571** (DAO); Mosquito Lake, QCI, 53°04′N, 132°07′W, 701 m, 24 Aug. 1957, *Calder & Taylor 23753** (DAO); Vict. Lk, QCI, 52°20′N, 131°28′W, 5 July 1964, *Calder & Taylor 35718** (DAO); Cumshewa Inlet, QCI, 52°55′N, 132°06′W, 213 m, 1 Aug. 1964, *Calder & Taylor 36507** (DAO); Brooks Peninsula, Vancouver Island, 50°10′N, 127°45′W, 853 m, Jul-1978, *Roemer 7884* (V); Brooks Peninsula, Vancouver Island, 50°10′N, 127°45′W, 853 m, Jul-1978, *Roemer 7890** (V); Chanal, Port, 53°36′N, 132°54′W, 0 m, Jul-1979, *Roemer 79159** (V); Brooks Peninsula, Cassiope Pond, Vancouver Island, 50°10′N, 127°45′W, 640 m, 7 July 1981, *Ogilvie, Hebda & Roemer 8173113** (V); Doom Mountain, 50°10′N, 127°46′W, 760 m, 17 Aug. 1981, *Ogilvie, Hebda & Roemer 8181711** (V); Cassiope Pond, 50°10′N, 127°45′W, 670 m, 2 Aug. 1981, *Ogilvie, Hebda & Roemer 818211* (V); Brooks Peninsula, Doom Mountain, Vancouver Island, 50°10′N, 127°46′W, 730 m, 5 Aug. 1981, *Ogilvie, Hebda & Roemer 818546* (V); Brooks Peninsula, Doom Mountain, Vancouver Island, 50°10′N, 127°46′W, 610 m, 7 Aug. 1981, *Ogilvie, Hebda & Roemer 818717* (V); Brooks Peninsula, Cladothamnus Lake, Vancouver Island, 50°09′N, 127°45′W, 730 m, 8 Aug. 1981, *Ogilvie, Hebda & Roemer 81894** (V); Louise Island, QCI, 52°57′N, 131°38′W, 835 m, 7 Aug. 1997, *Lomer & Grove 97239* (V); Graham Island, Mount Raymond, QCI, 53°16′N, 132°13′W, 975 m, 9 July 1997, *Lomer & Grove 97243* (V); Graham Island, Mount Stapleton, QCI, 53°15′N, 132°19′W, 880 m, 15 July 1997, *Lomer & Grove 97295* (V); Moresby Island, N side of Mount Moresby, QCI, 53°01′N, 132°13′W, 760 m, 15 July 1997, *Lomer & Grove 97312* (V); Graham Island, Mount Raymond, QCI, 53°16′N, 132°13′W, 975 m, 16 July 1997, *Lomer & Grove 97320* (V); Graham Island; Mount Tian, QCI, 53°48′N, 133°03′W, 487 m, 17 July 1997, *Lomer & Grove 97375* (V); Graham Island, QCI, 53°39′N, 132°44′W, 700 m, 17 July 1997, *Lomer & Grove 97378* (V); Dinan Creek, QCI, 53°39′N, 132°44′W, 700 m, 17 July 1997, *Lomer & Grove 97386** (V); Graham Island, QCI, 53°34′N, 132°43′W, 715 m, 16 July 1997, *Lomer & Grove 97394* (V); Apex Mountain, QCI, 52°42′N, 131°53′W, 914 m, 19 Aug. 1997, *Lomer & Grove 97448** (V); Graham Island, Mount LaPerouse, QCI, 53°14′N, 132°30′W, 1066 m, 20 Aug. 1997, *Lomer & Grove 97494* (V); Moresby Island, Mosquito Mountain, QCI, 53°01′N, 132°09′W, 792 m, 20 Aug. 1997, *Lomer &*

*Grove 97498** (V); Anna Lake, 50°30′N, 125°18′W, 25 Aug. 1992, *Ogilvie s.n.* (V); Mount Laysen, QCI, 52°41′N, 131°51′W, 950 m, 20 Aug. 1992, *Ogilvie s.n.* (V); Mount Laysen, QCI, 52°41′N, 131°51′W, 950 m, 20 Aug. 1992, *Ogilvie s.n.* (V); Moresby Island, Takakia Lake, QCI, 52°56′N, 132°04′W, 17 Aug. 1980, *Ogilvie s.n.* (V); Takakia Lake, QCI, 52°55′N, 132°03′W, 823 m, 19 Aug. 1980, *Ogilvie, Roemer & Mersereau s.n.* (V); USA, **Alaska: Aleutians West Co.:** Aleutian Islands: Akutan, 800 ft, 12 Aug. 1934, *L. Norberg, 610*, (MO); RUSSIA: **Kuril Archipelago**: Makanrushi, inland from Zakat Bay, 49°44′16″N 154°24′52″E, 100 ft., 18 Aug. 1997, *Sarah Gage SG4611** (WTU); Shumshu, about 2 km south of Pochtareva Cape, 50°49′07″N 156°29′31″E, 50 feet, 8 Aug. 1997, *Sarah Gage SG4212** (WTU); Paramushir, inland from Severo-Kurlisk by road, along eastern edge of Ebeko Volcano, 50°40′52″N 156°04′52″E, 1200 feet, 5 Aug. 1997, *Birgit Semsrott BS1178** (WTU); Ushishir Group, Yanchika Island, inland environs of Kraternaya Bay, 47°30′33″N 152°49′05″E, 1 Aug. 1997, *Sarah Gage SG4054** (WTU); inland environs of Kraternaya Bay, 47°31′10″N 152°49′08″E, 1 Aug. 1997, *Birgit Semsrott BS1087** (WTU); **Kamchatka:** Ust-Bolsheretskiy district, village of Ozernovskiy, *A. E. Kogevnikov s.n.** 1978 (V113790).

Calamagrostis tacomensis: USA:**Washington: Grays Harbor Co.:** Mt. Colonel Bob, Olympic Mts., 9 July 1931, *Thompson, 7330* (WTU); **Jefferson Co.:** Marmot Lake, 4000 ft, 23 Aug. 1935, *Dickinson 103* (OLYM); Marmot Lake, Olympic Mtns., 4000 ft, 23 Aug. 1935, *Dickinson 103* (WTU); McGravey Lake area, 15 Aug. 1990, *A. Comulada and P. Maurides* (OLYM); Mt. Olympus, 4000 ft., Aug.-07, *Flett 3075* (WTU); above Lake Constance, Olympic Mts., 6000 ft, 11 Aug. 1931, *Thompson 7869* (MO,US,WTU); Olympic mountains, 5000 ft, Aug. 1895, *C.V. Piper s.n.* (US); **King Co.:** Guy Peak, Cascade Mts., 3500 ft., 7 Aug. 1933, *Thompson 9686* (WTU); Guy Peak, Snoqualmie Pass, 3500 ft, 7 Aug. 1933, *Thompson 9686* (MO); Guy Peak, Snoqualmie Pass, 4000 ft 7 Aug. 1933 *Thompson, 9686**, (GH); **Kittitas Co.:** Beverly, 14 July 1977, *Creso 7-50* (Luth); head of Beverly Creek, Wenatchee Mtns., 2 Sept. 1933 *Thompson 10044**, (WTU); north fork of the Teanaway River, end of road, below Esmareldi Peaks, 4,500 ft., 21 July 1963, *Maas 1209** (WTU); **Lewis Co.:** Goat Rocks Primitive Area, 7000 ft, 6 Aug. 1940, *Thompson 15198* (MO); **Mason Co.:** Mt. Washington, 4500 ft, 11 Aug. 1985, *Maxwell 835* (Olym); **Pierce Co.:** Tipsoo Lake, Mount Rainier, 12 Sept. 1932, *Warren 1547* (WTU); Goat Mountains, 5 Aug. 1895, *Allen 177* (MO); Mt. Tacoma, 23 Aug. 01, *Flett, 1959* (WTU); Paradise Valley, Mt. Rainier, 5600 ft, 23 Aug. 1901, *Flett 1959* (NY); Paradise Lake, Mt. Rainier, 26 July 1931, *Thompson 7635* (WTU); Mount Tacoma, 25 Aug. 1901, *Flett 2076* (WTU); Alpine slopes on Governor Ridge, Mt. Rainier NP, 6000 ft, 27 Aug. 1931, *Thompson 8097* (US); Goat Pass, Mt. Rainier, 5500 ft, 26 July 1934, *Thompson 11079* (MO,WTU); Mount Rainier NP, nr. Klapatche Park, 3 Sept. 1975, *Creso & Leraas 5-19740* (Luth); Mt. Rainier, 6–7000 ft, Aug. 1895, *Piper s.n.*, (US); Silver Falls, Ohanapecosh, Mt. Rainier, 2200 ft, 31 July 19, *Flett s.n.* (US); west of Reflection Lake, Mt. Rainier, 17 July 19, *Flett s.n*, (US); Mount Rainier NP, along trail from Tipsoo L. to Dewey L., 13-Sep-1975, *Creso & Beck 5-858* (Luth); Mt. Wow, Rainier National Park, 5000 ft, 15 Aug. 1935, *Thompson 12593* (MO, WTU); Mt. Rainier, near Greenwater R., 15-Sep-1945, *Schallert 19582* (MO); Chinook Pass, Mt. Rainier National Park, 17 Aug. 1935 (WTU); Paradise Valley, *Parks & Parks 21045* (MO); Goat Mountains, 5 Aug. 1895, *Allen 177** (GH); Alpine slopes above Owyhigh Lakes, Mt. Rainier National Park, 5500 ft., 27 Aug. 1931, *Thompson 8097* (WTU); Mount Rainier NP, summit of Ipsut Pass, 28 July 1951, *M.C. Huntley s.n.* (Luth.); Mt. Rainier, Chinook Pass, 1900 m, 17 Aug. 1935, *Eyerdam s.n.* (MO); **Skamania Co.:** high mountains, 11 Aug. 1886, *Suksdorf 201* (US); 11 Aug. 1886, *Suksdorf, 909*, (MO, NY); high mountains, 27 Aug. 1890, *Suksdorf 1025* (MO,US); Pumice Plain north of crater breach, Mount St. Helens, 4 Aug. 1994, *Titus s.n.* (WTU); Camp 19, 4 Aug. 1899, *Flett 1390* (WTU); 27 Aug. 1890, *Suksdorf s.n.* (US); Columbia National Forest. Along Wind R., 1600 ft, 20 May 1926, *Ingram 2022** (OSU); **Snohomish Co.:** Perry Creek, 25 July 1983, *Hagen s.n.* (WTU); **Yakima Co.:** Chinook Pass, Cascade Mtns., 5500 ft., 1 Aug. 1940, *Thompson 15149* (WTU); **Oregon: Harney Co.:** Steens Mts. Region 11.5 mi E and 10 mi due S of Frenchglen, T33S R32 3/4E sec 26, 6200 ft, 25 July 1954, *Hansen 893** (OSU); Steens Mountains, 7120 ft, 5 Aug. 1992, *Mansfield 92-19449** (OSU).

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REVIEWS

Tending the Wild: Native American Knowledge and the Management of California's Natural Resources. By M. KAT ANDERSON. 2005. University of California Press, Berkeley. 555 pp. $50.00 (cloth). ISBN 0-520-23856-7. $19.95 (paper). ISBN 0-520-24851-1.

Among botanists and ecologists, the prevailing view has long been that Native American populations were too small, too dispersed, and too low-tech to have had much impact on California's native landscape. The fact that forests have encroached on Yosemite Valley meadows, and dead brush has built up to fuel catastrophic wildfires in many areas only since depopulation and decline of traditional practices among indigenous peoples has received little serious attention among those seeking to understand the flora and vegetation of our state.

More than a decade ago, an edited volume of papers on environmental management by Native Californians (Blackburn and Anderson 1993) quietly entered the scene. Anthropologists and ethnobotanists working independently in different areas had been finding indications that indigenous non-agricultural peoples systematically modified their surroundings. Taken together, the several papers on this theme did attract some notice, and researchers in other fields began to look at Native Americans' relationships with the land in a new light.

That was just an initial step. Now comes its apotheosis in an important new book, *Tending the Wild.* In this truly impressive work, ecologist M. Kat Anderson presents overwhelming evidence that California Indians—though often simplistically classed as "hunter-gatherers"—were unquestionably a powerful force in the history of California's flora and plant communities. The stunning wildflower displays and park-like woodlands filled with astonishingly abundant wildlife that dazzled early explorers and settlers were not, as they assumed, a pristine wilderness untouched by human hands. These were, in fact, anthropogenic landscapes.

As Anderson shows, some three hundred thousand indigenous people throughout the state could and did have profound effects as they selectively burned, pruned, weeded, tilled, scattered seeds, and harvested the results of their efforts over the course of many centuries. The long duration and broad scale of these practices demonstrably affected the diversity, abundance, distribution, physical structure and health of both plants and the ecosystems of which they are a part.

The book presents an enormous quantity of evidence derived from widely varied sources. Thorough examination of the historical, ethnographic and ecological literature provides information that is fairly compelling in itself, but that's only one part of it. Also cited are the vivid words of living Native elders themselves, from their own memories and in accounts passed down to them from earlier generations, based on interviews and fieldwork Anderson conducted among the Sierra Miwok and Mono. They clearly show that systematic management—particularly through burning—was pervasive, and that the landscape has changed and resources are less healthy now that people are no longer taking care of them in the old way.

Anderson and others have conducted field experiments replicating indigenous harvesting, burning, and pruning techniques to determine their effects on resource productivity in light of plants' responses to such disturbance. Among the most compelling lines of evidence are her studies of museum collections of cultural artifacts—visible proof that almost unimaginable quantities of unbranched shoots and rhizomes, which could only come from managed plants, were required to create the thousands of baskets and miles of hand-twisted cordage utilized by even a single Native village.

The book is divided into three principal sections. The first paints a picture of California's "natural" abundance as described by early visitors, summarizes indigenous peoples' place in and utilization of that world, and describes both cultural and environmental changes after European contact. The second part, "Indigenous Land Management and its Ecological Basis," systematically presents and analyzes the various methods California Indians used to enhance productivity of specific culturally important resources. The final section discusses the perpetuation of some of these practices by Native people today and the lessons they may have for landscape restoration.

Fire suppression (with concomitant changes in vegetation) actively began around the turn of the last century in the Sierra and central California, where Anderson did much of her field research. Indian burning was forcibly terminated about a hundred years earlier throughout the large part of coastal California affected by the mission system (Timbrook et al. 1982). In many areas, therefore, indigenous fire management practices are no longer living in cultural memory, making their revival a challenging task. It is a worthwhile task nonethe-

less, and Anderson offers suggestions and guidelines about how this might be approached on a case-by-case basis in order to restore sustainable ecosystems.

Plant-oriented readers may note a few instances of hyperbole. For example, although it is well established that humans have been living in California for at least 13,000 years, Anderson provides no real archaeological or other evidence to support her assertion that they were actively managing resources for all that time. It is likely that these management practices were carried on for at least centuries and possibly millennia, but their actual antiquity remains unknown. She also sometimes seems a bit too attached to the concept of the ecological Indian living in harmony with the environment, waving aside the documented instances of overexploitation and extirpation in prehistory. I hope these few failings will not distract anyone from the important contributions of this work.

Obviously, there are many factors at play in the changes California's landscape has undergone since European contact—introduced weeds, livestock grazing, and various land-use practices by non-Indians to name a few—but it is clear that Native American management systems have played a significant role too long unrecognized in the vegetation history of our state.

All the more appealing because it is very well written, this book would make an excellent text for all manner of anthropology, botany, ecology, and forestry classes. It is also a useful reference work, nearly a third of it devoted to a thorough index, a large bibliography, and endnotes offering copious citations for virtually every paragraph. There are also 3 maps, 44 illustrations, and 12 tables. All California botanists, plant ecologists and land managers should seek out, read, and pay attention to *Tending the Wild.*

—JAN TIMBROOK, Santa Barbara Museum of Natural History, 2559 Puesta del Sol Road, Santa Barbara, CA 93105. Email: jtimbrook@sbnature2.org.

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CALIFORNIA BOTANICAL SOCIETY
2006–2007 SCHEDULE OF SPEAKERS

7:00 p.m. on the 3rd Thursday of the month
2063Valley Life Sciences Building
University of California, Berkeley

September 21	Invasive Spartina in San Francisco Bay: the trouble with hybrids Debra Ayres, Evolution and Ecology, University of California, Davis
October 19	Comparative water relations of semi-arid plant communities in California and Mexico Radika Bhaskar, Department of Biological Sciences, Stanford University, Stanford
November 16	The diversification of the world's redwoods: California and beyond Jarmila Pittermann, Department of integrative Biology, University of California, Berkeley http://ib.berkeley.edu/labs/dawson/generate_person.php?name=+Jarmila+Pittermann
February 17	Annual Banquet & Graduate Student Meeting California Polytechnic State University, San Luis Obispo Out of the past and into the future: Response of high-elevation Sierra Nevada forests to climate change Constance I. Millar, Sierra Nevada Research Center, USDA Forest Service, Albany
March 15	The evolution of floristic modeling Barbara Ertter, Curator of Western North American Flora, University and Jepson Herbaria, University of California, Berkeley http://ucjeps.berkeley.edu/people/ertter.html
April 19	Functional diversity and alien grass impacts in a threatened dry forest ecosystem of Hawaii Darren Sandquist, Department of Biological Science, California State University, Fullerton http://biology.fullerton.edu/people/faculty/darren-sandquist/index2.html

Lectures are open to all. Refreshments will be served before and after the seminars. Information and reservation forms for the annual banquet will be mailed to members. Non-members are welcome. For registration forms and additional information please call 510/643-7008 or visit our website (www.calbotsoc.org).

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THE IMPORTANCE OF LAYERING IN THE RAPID SPREAD OF *ARUNDO DONAX* (GIANT REED)

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ABSTRACT

Arundo donax L. (Poaceae) is an invasive, perennial grass that grows in many-stemmed, cane-like clumps. It does not produce viable seeds in California and is currently thought to invade habitats rapidly by rhizomes and fragments only. But, during a two-year field study in the Tijuana River Valley, California, expansion of *A. donax* clumps via rhizomes was slow, only 0.29 m 2 yr^{-1}, and new recruits from fragments were rare, only 4.7 ha^{-1} yr^{-1}. Whereas layering, a mode of spread heretofore ignored by researchers, was common in the flood zone. Layering is the adventitious sprouting of stem tips in contact with the ground. Layering can be considered to be both expansion of a clump (while the layering stem is still alive and attached to the clump) and asexual reproduction (after the layering stem dies). When viewed as clump expansion, layering was 7.4 times faster than the annual expansion via rhizomes. When viewed as reproduction, layering produced 25 times more new recruits than fragments. Layering was therefore an important means by which *A. donax* was spreading within the flood zone.

A new general view of *A. donax* invasion is presented illustrating that fragmentation is the means by which *A. donax* invades a new site in the flood zone, expansion via rhizomes maintains an *A. donax* clump, and layering is the means by which *A. donax* spreads quickly and episodically within the flood zone. Outside the flood zone, *A. donax* expands slowly via rhizomes only and no new recruits arrive from either fragmentation or layering.

The Tijuana River Valley results challenge the current "top-down" management policy, which presumes that most new recruits come from upstream and that all clumps expand at the same rate. The results show that, on the contrary, most new recruits come from within the habitat, via layering, and that clumps in the flood zone expand faster than those outside the flood zone. I conclude that the top-down policy is counter-productive and suggest that managers shift to controlling *A. donax* "inside-out," i.e., conduct treatments first inside and then outside the flood zone. In this way, the fastest expanding clumps – those in the flood zone – will be treated first.

Key Words: *Arundo donax*, giant reed, layering, spread, plant fragments, rhizomes, top-down, inside-out.

Arundo donax L. (Poaceae), giant reed, is a large perennial grass from the Mediterranean region that has become a serious pest in tropical and temperate parts of the world and is now on the list of the 100 World's Worst Alien Species (Global Invasive Species Database 2005). In California it is known to severely degrade wildlands by altering vegetation structure, displacing native plant species, reducing habitat quality for native animal species, and increasing fire frequencies (Dudley 2000). *Arundo donax* is particularly damaging in California's riparian habitats because these are already "endangered" due to losses from channelization, damming, development and agriculture (Faber et al. 1989). An enormous amount of effort and millions of dollars are currently being expended controlling *A. donax* in riparian habitats in California (e.g., Katagi et al. 2002).

In order to prioritize sites and determine the best control methods, one needs detailed knowledge of the means of spread of an invasive species (Radosevich et al. 1997; Bryson and Carter 2004). Unfortunately, as several authors have complained (Hoshovsky 2003; McWilliams 2004), there are few studies of the basic biology of *A. donax*. If we divide spread into the expansion of existing plants and the establishment of new recruits, we find that neither has been well studied.

Most authors note that *A. donax* expands rapidly once established and they presume that it is via rhizomes (Else 1996; DiTomaso 1998), but there has not been a published field study that has measured the lateral expansion of clumps of *A. donax*. Instead studies have focused on the vertical growth of a single stem – under normal conditions (Perdue 1958), after a fire (Rieger and Kreager 1989) and under various lab conditions (e.g., Motamed and Wijte 1998; Boose and Holt 1999; Decruyenaere and Holt 2001).

Arundo donax reproduction studies are also rare. In California, *A. donax* does not produce viable seed (Perdue 1958; Bell 1993) and therefore does not reproduce sexually. It is currently believed that asexual reproduction through fragmentation is the primary method of establishment of new plants (e.g., Bell 1997). Else (1996)

found new recruits from fragments to be common in the lower reaches of Santa Margarita River. From that observation the current view of the reproduction and dispersal of *A. donax* has developed:

> Flood events break up clumps of *A. donax* and spread the pieces downstream. Fragmented stem nodes and rhizomes can take root and establish as new plant clones. Thus invasion, spread, and therefore management, of A. donax is essentially an intra-basin and downstream phenomenon.
> (Bell 1997; see also Else 1996; DiTomaso 1998).

This view that plant fragments drive the reproduction and dispersal of *A. donax* plays an important role in determining management policies. In particular, the emphasis on invasion from upstream has led to the policy of conducting control activities from the "top-down" in a watershed (e.g., Else 1996; Vartanian 1998). This policy has, in turn, driven management activities and funding decisions. Yet the top-down policy is based on very few data — mainly anecdotal evidence and the surveys by Else (1996), which were conducted during only one month at only one watershed. The extensive control effort being waged against this plant calls for more studies of its spread so that the empirical basis of management policies can be strengthened.

The main goals of this paper are to: (1) describe the lateral expansion of established *A. donax* clumps in the wildlands of the Tijuana River Valley; (2) examine the mechanisms and frequency of establishment of new clumps within the valley; (3) compare the observed spread with that predicted by the current literature; and (4) suggest changes to the current management policies.

Study Site

The Tijuana River Valley is a valuable wildland within urban Greater San Diego (Fig. 1). The valley is a coastal flood plain at the downstream terminus of the 448,000 ha Tijuana River watershed (Concur 2000). The valley stretches from the international border crossing at San Ysidro to the ocean at Imperial Beach and spans 1,457 ha at approximately sea-level (Southwest Wetlands Interpretive Association 2002). It consists of riparian, coastal sage scrub, freshwater, tidal estuarine channels, and coastal salt marsh habitats. The valley is mostly public land and includes a county regional park, a state park, a national wildlife refuge, and an estuary that is a designated National Estuarine Research Reserve and Ramsar Wetland of International Importance.

Several invasive, non-native plants are present in the valley, including *A. donax*, salt cedar (*Tamarix* spp.), and castor bean (*Ricinus communis* L.). Managers of the public lands considered these invasive species a major threat to the sensitive ecosystems within the valley (Concur 2000) and an invasive plant control program was begun in 2002 (Southwest Wetlands Interpretive Association 2002; Boland 2004). A study of the invasive species found that *A. donax* was particularly abundant on the edges of the dense willow forest and occupied approximately 17 of the total 1,457 ha (Southwest Wetlands Interpretive Association 2002). In addition, *A donax* was common upstream in Mexico (Woch 2005).

This study was started in May 2003, ran for two years, and was influenced by three rainfall seasons. The 2002–2003 season had an average amount of rainfall (27.0 cm in San Diego), the 2003–2004 season was relatively dry (13.2 cm), and the 2004–2005 rainfall season was the third wettest in San Diego history with a total of 57.2 cm of rain (Western Regional Climate Center 2005). The unusually heavy rainfall in San Diego produced only moderately heavy flows in the Tijuana River Valley because the upstream dams were refilling after several dry years. Flow rates in the valley have been collected since 1962, and the 2004–2005 flood season was a 1-in-5-year event for flood duration (number of days when flows were >10 m^3 sec^{-1}), and a 1-in-9-year event for maximum flow (International Boundary & Water Commission 2006).

In this paper, I use the term "flood plain" to mean the relatively flat area that borders the river and is subject to flooding, and the term "flood zone" to mean the part of the flood plain that was actually flooded the previous winter. The flood zone may also be called the "active floodplain." The size of the flood zone varies from year-to-year and was widest, during this study, in the winter of 2004–2005.

Arundo donax

A. donax is a reed-like perennial grass that grows in large clumps, or patches, many meters across and several meters tall (Fig. 2). The clump is composed of: mature branched stems, or culms, (A); younger, unbranched stems (B); rhizomes or root-stock (D); and roots (E). It also includes many standing dead stems, both branched and unbranched (C).

The clump does not produce viable seeds in California and spreads via rhizomes (D), fragments (F) and layers (G). Fragmentation occurs when a piece of a plant, either rhizome, stem or branch, breaks off the original clump and grows into a new plant elsewhere (Else 1996; DiTomaso 1998; Cronk and Fennessy 2001; Decruyenaere and Holt 2001). Layering, also called tip-layering

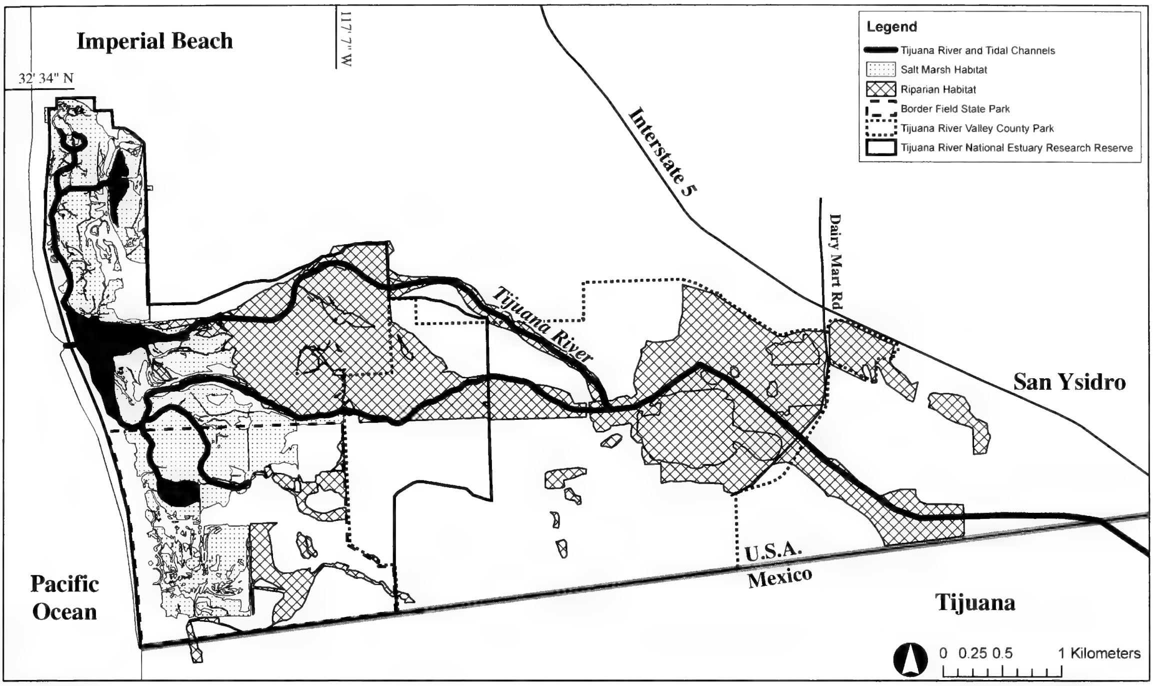

FIG. 1. Map of Tijuana River Valley showing the main habitat types and the boundaries of the parks and research reserve.

or ground-layering, occurs when a normal stem forms roots and shoots adventitiously where it contacts the soil (Grace 1993). Because the layering stem is frequently embedded in mud it usually dies within a few months leaving a fully independent young plant several meters from the original clump (personal observation).

The three means by which *A. donax* invades space – rhizomes, fragments, and layers – are a mix of asexual reproduction and growth. Asexual reproduction is defined as the "numerical increase in physiologically independent plant units by clonal means" (Grace 1993). Fragmentation is therefore clearly asexual reproduction because an independent plant is formed. The expansion of an *A. donax* clump via rhizomes is clearly vegetative growth because rhizomes are long-lived and the stems growing from the rhizomes remain interconnected. On the other hand, layering can be considered both expansion of a clump and asexual reproduction; it is expansion when the layering stem is still alive because the layer is still attached to the clump, and it is asexual reproduction when the layering stem dies, because the new shoots have become an independent plant. Because of the dual nature of layering, I examined it as both expansion of a clump (along with rhizomes) and as asexual reproduction (along with fragments).

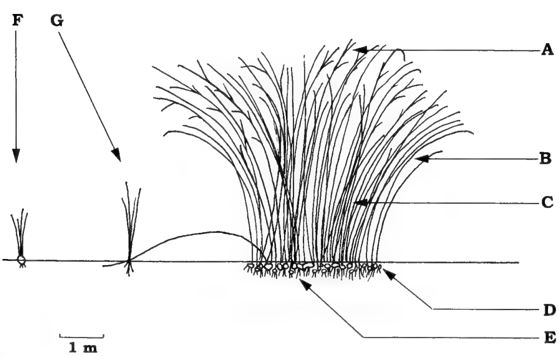

FIG. 2. Diagram of a clump of *A. donax* showing its various structures including the creation of new clumps via layering and fragmentation. See text for explanation of the letters.

METHODS

Expansion of Clumps via Rhizomes

The lateral expansion of *A. donax* via rhizomes was monitored for two years at 19 clumps in the Tijuana River Valley. The clumps were randomly chosen using a cluster sampling design; 9 occurred inside and 10 outside the flood zone of 2005. The clumps were roughly circular and the basal circumference of each clump was measured using measuring tape and converted to basal diameter; the average starting basal diameter was 5.5 m (std. dev. = 2.4; range = 2.1–11.8 m; n = 19). In order to monitor horizontal expansion of each clump, two stakes were driven into the soil

at the leading edge of the upright stems. The stakes were placed on either side of the clump on a randomly chosen diameter – either in a north-south or east-west direction. The stakes were placed, numbered, and photographed in May 2003, and revisited in May 2004 and May 2005. During revisits, the expansion outwards from the stake (i.e., the distance between the stake and furthest new stem) was measured with a meter stick. The expansion of each clump over two years is reported as the average of the May 2005 measurements made at that clump's stakes (± 1 SE). Three stakes at three different clumps were lost through vandalism; therefore three clumps are represented by a single May 2005 measurement. The expansion rates of the clumps inside and outside the flood zone were compared using a t-test (F-test indicated homogeneity of variances; $p = 0.01$).

Expansion of Clumps via Layering

Expansion via layering was measured at the 19 monitored clumps for two years (May 2003–May 2005). During each visit, the entire periphery of the clump was searched for newly established plants from layers. Each new recruit was excavated and determined to be a layer if it was clearly growing from a stem that was still attached to the parent plant. When a layer was found, the most distant shoot on the layer was labeled with flagging tape, and its distance from the clump was measured. The average distance of expansion via layers was calculated for the clumps that produced layers ($n = 6$) and this was compared to the average distance of expansion via rhizomes at the same clumps using the Wilcoxon two-sample test (data are presented as means ± 1 std. err.). The non-parametric test was used because the F-test indicated that the variances were not homogeneous ($p > 0.05$).

Frequency of Layering Clumps in the Valley

A survey was also conducted to determine the frequency of layering clumps in the valley as a whole. The proportion of clumps expanding via layers during 2005 was estimated by sampling at ten sites throughout the valley during August 2005. The sites, five inside and five outside the flood zone of 2005, were chosen in a stratified-random manner. At each site, a westward transect was walked and every *A. donax* clump within 15 m was examined until a total of 20 clumps had been reached. At each clump the entire periphery was searched for newly established plants from layers. A new recruit was considered to be a layer only if it was clearly growing from a stem that was still attached to the parent plant. [Old layers, which have many, tall stems and thick rhizomes, were not included in the counts.] Each clump was tallied as either having: 0, 1–4, or >4 layers. A total of 100 flood zone and 100 outside-flood zone clumps were examined in this way.

Density of New Recruits from Fragments and Layers

The valley was surveyed for new recruits during June 2005 using the same procedures as Else (1996). Eight transects across the river valley were chosen in a stratified-random manner. The transects were 2 m-wide belts which ran perpendicular to the river channel and extended from the southern edge to the northern edge of the 2005 flood zone. The boundary of the flood zone was determined by the presence of debris indicating the highest flood level of the 2004–2005 flood season. The lengths of the transects varied depending on the width of the flood zone (range $= 97$–865 m; $n = 8$). The total area surveyed was 0.84 ha. Within the transect, the length of each established *A. donax* adult was measured and the numbers of new *A. donax* recruits from fragments and layers were counted. Each new recruit was excavated and determined to be a layer if it was clearly growing from a stem that was still attached to the parent plant, or a fragment if it was growing from a plant part that was not attached to the parent plant. Non-parametric tests were used on these data. The Wilcoxon's signed-rank test was used to test for differences between the numbers of new recruits from fragments and those from layers within the transects ($n = 8$ transects), and the Chi-square Test with Yates' correction was used to test for differences between the total numbers of recruits from fragments in these transects (0.84 ha) and in the transects conducted at Santa Margarita River by Else (1996; 0.70 ha). The average density of new recruits from fragments and layers in the valley was estimated from these surveys and is reported as the number per hectare.

When only a few new recruits from fragments were found in the whole-valley surveys a second set of surveys was conducted during June 2005 in the eastern part of the valley around the Dairy Mart Road Bridge. The Tijuana River enters the valley in the east and the first obstacles to its flow are the bridge and the willow forest nearby. The site had many debris piles and if fragments were abundant anywhere in the valley they were expected to be common there. Five survey areas, each 100 m $\times$ 50 m, were placed around the bridge and in the forest. Within each survey area, six randomly-chosen belt transects (2 m wide $\times$ 50 m long) were surveyed using the same procedures as described above, i.e., along the transects, the length of established *A. donax* adults was measured and new *A. donax* recruits were excavated, determined to be fragments or

FIG. 3. Photograph of a layering stem. The stem (coming in from the left) has become buried and has formed new shoots, rhizomes and roots adventitiously at a buried node. This layer was produced in open space 6 m from the parent clump and was 0.6 m tall. (A blackboard has been placed in the background.)

layers, and counted. A total area of 0.3 ha was surveyed in this eastern site.

RESULTS

Expansion of Clumps via Rhizomes

Of the 19 *A. donax* clumps monitored in 2003, all were alive when re-examined in 2004 and 2005. Nine of the clumps had been inundated by flooding that occurred during the record rains of 2004–2005 but none was damaged; the only obvious changes were that some of the standing dead stems had been removed and sedimentation (up to 15 cm at the stakes) had occurred. There were no obvious changes to the ten clumps that had not been inundated.

The *A. donax* clumps expanded slowly via rhizomes. Over the two years of monitoring the mean expansion of the basal edge of a clump was only 0.29 ± 0.04 m 2 yr^{-1} (range = 0–0.63 m; n = 19). The two-year expansion rates were significantly faster at clumps that were growing inside the flood zone (mean = 0.41 ± 0.05 m 2 yr^{-1}; n = 9) than those growing outside the flood zone (mean = 0.18 ± 0.04 m 2 yr^{-1}; n = 10; t-test $p < 0.01$).

Expansion of Clumps via Layering

No layers were formed at monitored clumps during the relatively dry winters of 2002–2003 and 2003–2004, when the clumps were not inundated by floodwaters. But, during the wet winter of 2004–2005, 80 layers were formed at the inundated monitored clumps. Layers were typically formed when an attached stem bent over or fell over and flooding caused its tip to become embedded in wet mud; within a few weeks the embedded nodes sprouted stems and roots, and then grew into new, multi-stemmed plants (Fig. 3). The layers tended to be produced at the edge of the canopy and the average distance of the layers from the base of the monitored clump was 3.31 ± 0.40 m (n = 6) for the clumps that produced layers. This expansion distance was significantly greater than the average distance of expansion via rhizomes at the same clumps over the two years (0.45 ± 0.06 m 2 yr^{-1}; n = 6; Wilcoxon two-sample test; $p < .005$).

TABLE 1. THE DENSITY OF *A. DONAX* RECRUITS FROM FRAGMENTS AND LAYERS IN SURVEYS CONDUCTED IN THE SANTA MARGARITA RIVER (ELSE 1996) AND THE TIJUANA RIVER VALLEY. Else (1996) did not count layers.

Site	Santa Margarita River	Tijuana River Valley – entire valley	Tijuana River Valley – eastern river
Source	Else (1996)	this study	this study
Survey area (ha)	0.697	0.837	0.300
Established *A. donax* % cover	—	10%	1%
A. donax recruitment from fragments			
Fragments (#)	69	4	1
Fragments per ha	98.9	4.7	3.3
A. donax recruitment from layers			
Layers (#)	—	99	6
Layers per ha	—	118.2	20.0

These data show that some clumps within the flood zone expanded rapidly by producing many distant layers.

Frequency of Layering Clumps in the Valley

The valley-wide surveys of clumps provided a broad measure of the frequency of layering in the valley and in particular a measure of the proportion of clumps undergoing rapid expansion. Inside the flood zone, layering was common: 88% of the randomly chosen clumps had layers (79% had >4 layers; 9% had 1–4 layers; 12% had 0 layers; n = 100 clumps). Outside the flood zone, all clumps had 0 layers (n = 100 clumps). These results show that layering only occurred within the flood zone and that most clumps inside the flood zone spread quickly by producing many layers.

Density of New Recruits from Fragments and Layers

The belt surveys showed that new *A. donax* recruits growing from fragments were rare in the Tijuana River Valley. Only four were present in the transect surveys of the entire valley (Table 1). This was significantly fewer than the 69 recruits from fragments counted by Else (1996) over a smaller area in the Santa Margarita River (Table 1; Chi-square Test with Yates' correction; $p < .005$). Even at the eastern river site within the Tijuana River Valley, where I expected fragments to be abundant, only one was present.

On the other hand, the belt surveys confirmed that new *A. donax* recruits growing from layers were common in the Tijuana River Valley. Ninety-nine layers were present along transects across the entire valley (i.e., within 0.84 ha) making layers 25 times more common than recruits from fragments (Table 1). This difference was statistically significant (Wilcoxon's signed-rank test; $n = 8$ transects; $p < .01$). Because layers are produced by established adults, it might be presumed that where adults are rare layering would be relatively unimportant. But in the eastern river, where established *A. donax* clumps were rare (only 1% cover), there were more new recruits from layers than from fragments (Table 1).

DISCUSSION

Spread of *A. donax* by Rhizomes, Fragmentation and Layering

The current view of *A. donax* spread is that it is fast and accomplished by rhizomes and fragments only (e.g., Dudley 2000). As pointed out by Hoshovsky (2003) and McWilliams (2004) this view is based on mainly anecdotal evidence and little published field data (cf. Else 1996). In this two-year study within the Tijuana River Valley I found that *A. donax* expanded slowly via rhizomes, and new recruits from fragments were rare; but layering was common and layering resulted in clumps expanding quickly and adding many new recruits. These findings show that there needs to be a re-evaluation of spread by *A. donax* and the roles played by its different plant parts – rhizomes, fragments and layers.

The thick, short-noded, many-branched rhizomes of *A. donax* consolidate space rather than quickly invade new space. The fastest expansion via rhizomes was in the flood zone and averaged only 0.41 $m^2\ yr^{-1}$. Although not expanding quickly, rhizomes are constantly reinvading space within their own clumps and sending up more stems within the clump which results in clumps becoming more dense and there being no "dead center" (personal observations). *Arundo donax* rhizomes appear to fit the description of "pachymorphic" rhizomes, which are designed for carbohydrate storage, and protection from fire, frost, grazers, and desiccation, rather than for fast expansion (Cronk and Fennessy 2001).

Fragments did produce new recruits within the flood zone of the Tijuana River Valley but they were rare in comparison to the number found along the Santa Margarita River by Else (1996).

Considering that conditions were ideal for the production of many new fragment recruits – 2004–2005 had a long and wet rainy season – this may be close to the maximum invasion density for the valley. Fragments are likely to be important in the long-distance dispersal of *A. donax* but, at these densities, they cannot account for the fast spread of *A. donax* within a site.

Layering was common in the flood zone of the Tijuana River Valley during 2005; most of the randomly-chosen clumps in the flood zone had five or more layers. By Grace's (1993) definition of asexual reproduction, layering is first expansion of a clump (like rhizome growth) and then asexual reproduction (like fragmentation). When viewed as expansion, layering was 7.4 times faster than the annual expansion via rhizomes, and when viewed as reproduction, layering produced 25 times more new recruits than fragments. It is clear that layering was an important means by which *A. donax* spread in the flood zone.

How frequently *A. donax* clumps expand at this rate is unknown. It is possible that abundant layering occurs only when rainfall is sufficient to bend stems and flooding is sufficient to produce enough sedimentation to bury stem tips. The 2004–2005 flooding was a 1-in-5 to 1-in-9-year event (International Boundary & Water Commission 2006) and abundant layering may therefore be as episodic as once every 5 to 9 yrs. Even at this frequency, layering would result in faster expansion of clumps than rhizomes, and more new recruits than fragments.

Layering is a common trait of many invasive plants (Reichard 1996), and is important in the spread of several invasive species including, *Rosa multiflora* Englm. (Gleason and Cronquist 1991), *Cotoneaster* spp. (Sigg 2000), *Rubus discolor* Weihe & Nees (Hoshovsky 2000), and *Lonicera japonica* Thunb. (Florida Exotic Pest Plant Council 2003). But layering has been largely ignored in the *A. donax* literature; it is not mentioned at all in papers that have focused on spread, e.g., Bell 1993; Else 1996; Bell 1997; DiTomaso 1998; and Hoshovsky 2003. Dudley (2000) in his excellent review of the literature on *A. donax* did describe layering, i.e., "*root formation does occur where an attached culm has fallen over and is in contact with the substrate*," but went on to say that *A. donax* "*spreads vegetatively either by rhizomes or fragments*" leaving out layering entirely.

I suggest the following general history of *A. donax* invasion into a section of flood zone at a site like the Tijuana River Valley (Fig. 4). It is based on the results of this paper and describes the invasion over approximately 10 yrs showing when the different plant structures (fragments, rhizomes, and layers) are important. The starting point is an idealized section of flood zone with a permanent pool (left), a stand of dense willows

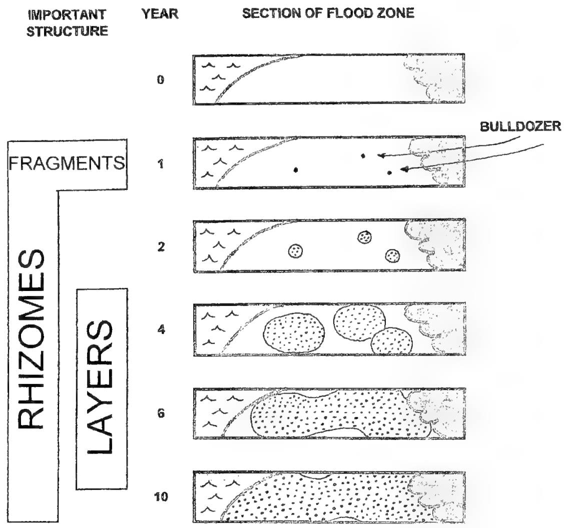

FIG. 4. General history of *A. donax* invasion into an idealized portion of flood zone over 10 yrs showing when the different plant structures (fragments, rhizomes, and layers) are important.

(right) and some open ground with low-growing annuals (center). A bulldozer disturbs an *A. donax* stand upstream and during Year 1 three rhizome fragments are washed into the site. [Bulldozers appear to be the most common cause of clump break-up and rhizomes are the most viable plant fragments (Boland unpublished data).] Fragments, although rare, are important in the initial invasion of a large area of bare space. The fragments become established and slowly expand via growth of their rhizomes to become small clumps.

By Year 4 the clumps' stems are long enough to bend over and touch the ground and they start producing layers. Many layers are produced during favorable years and the clumps expand rapidly and episodically via layering during the next few years. Layering is important as a means of rapidly invading open space near the clump. But there are barriers to the spread via layering – layers do not form in permanent pools of water and stems cannot lay down in dense willows or dense *A. donax*. Therefore *A. donax* does not enter the pool or the dense willows.

Finally, the entire open space is taken over by *A. donax*, which is being maintained by the continuous expansion of rhizomes only. Each plant structure plays a different role in the invasion: fragments provide the initial long-distance dispersal; rhizomes maintain the clump; and layers carry out the fast spread into open space.

In dry sites, outside the flood zone, the history is less dynamic; *A. donax* clumps expand slowly outwards via rhizomes only. There are no new recruits from layers or from fragments. These areas remain strikingly similar from year to year.

The history described in Fig. 4 comprises a new vision of the dynamics of *A. donax* at a flood zone site in southern California. There are three important points in this new vision (compare with Else 1996; Bell 1997; Dudley 2000). First, recruitment via fragments is less common than previously reported, and fast spread is not due to frequent new invasions via fragments. Second, layering is more common than recognized and clumps use layering to quickly invade open space. And third, because layering is the production of new recruits by the existing clumps, the majority of new recruits come from within the site rather than from outside the site, i.e., most recruits come from layers, not from fragments.

Recruits from Fragments: Tijuana River Valley v. Santa Margarita River

Fragments have been considered the primary mechanism of *A. donax* invasion because Else (1996) found them to be abundant in the Santa Margarita River (Bell 1997; DiTomaso 1998; Dudley 2000). But fragments were not abundant in the Tijuana River Valley, not even in the eastern river site where one would have expected them to be common among the debris trapped at the bridge and in the forest. This was not because conditions were poor for the production of fragments – the significant rainfall of 2004–5 should have produced ideal conditions for recruitment via fragments.

I propose two hypotheses to account for the significant difference in density of recruitment from fragments in the two rivers. First, I suggest that the invasion rates Else (1996) obtained were unusually high because intensive *A. donax* control activities were being conducted on the Santa Margarita River at the time. These control activities included the mechanical removal of whole *A. donax* clumps (roots, rhizomes and stems), the grinding of the material in a tubgrinder, and the return of the ground material to the site without herbicide application (Slader Buck personal communication). The chances that living pieces of *A. donax*, particularly rhizomes, accidentally escaped these activities were high. I suggest that these fragments were washed downstream by the winter floods of 1994–1995 and that when Else (1996) did her surveys in July 1995 she counted unnaturally high densities of recruits from fragments. Support for this hypothesis comes from descriptions of later mechanical removal operations in the same watershed; Giessow and Giessow (1999) found high densities of recruits from fragments in an area where mechanical removal had been used and wrote that "*most of the* Arundo *resprouts that occurred resulted from small pieces of rhizome that broke off during the mechanical removal process.*" In addition, the rainfall during the season before Else's surveys was 71% above average (Western Regional Climate Center 2005). There was therefore more than sufficient rainfall to disperse the fragments and to provide moist conditions for their successful recruitment. I suggest that these circumstances combined to produce an unnaturally high number of new recruits from fragments in the areas that Else surveyed in Santa Margarita River in July 1995.

Second, it is also possible that the invasion rate at Santa Margarita River was high because there are no dams on the river to block the downstream flow of water-borne propagules, whereas most of the other major watersheds in southern California, including Tijuana River, are dammed. It is possible that dams are important barriers to the dispersal of the water-borne propagules of *A. donax*.

These hypotheses are not mutually exclusive, both may be correct, and both may explain some of the observed difference in the recruitment rates at Tijuana River and Santa Margarita River. It is clear that more research needs to be done on recruitment rates at these and other sites, and on the influence of dams and mechanical treatment techniques on fragment recruitment downstream. But, it appears that the general importance of fragments in the spread of *A. donax* may have been exaggerated because of where and when Else (1996) did her study.

Strategy for the Control of *A. donax*

New information about the spread of an invasive species inevitably leads to a re-evaluation of the strategies being used to control that species. The current management strategy for the control of *A. donax* is to use mainly chemical treatments and to begin in the upper watershed and progressively work downstream (i.e., "top-down;" e.g., Else 1996; Vartanian 1998). This strategy is based on the assumption that *A. donax* clumps are constantly producing abundant fragments that invade downstream sites; thus, one should eliminate the upstream source of recruits before treating plants downstream. This assumption, however, is only partly correct; in the Tijuana River Valley, new recruits from fragments did occur but they were relatively rare. Instead, layering by existing clumps created the vast majority of the new recruits in the flood zone. A space in the Tijuana River flood plain was 25 times more likely to be invaded by a layer from within than by a fragment from without (Table 1). Even at sites where *A. donax* was rare (i.e., only 1% cover), recruitment from layers was more common than recruitment from fragments. Therefore, the spread of *A. donax*, contrary to the current view (e.g., Bell 1997 quoted in the Introduction), was mostly a within-site phenomenon rather than a downstream phenomenon.

The top-down policy is also based on a second, but unstated, assumption that all clumps of *A. donax* are expanding at an equal rate. The Tijuana River Valley results show that this assumption is not correct; *A. donax* clumps inside the flood zone expanded more quickly, via both rhizomes and layers, than clumps outside the flood zone.

The two assumptions that are the basis for the top-down policy are therefore not valid and the top-down approach is actually counter-productive. The control of *A. donax* is expensive and slow, and one finds that under the top-down approach, while controlling some slow-expanding *A. donax* in the upper reaches, other clumps are rapidly expanding into open space in the lower reaches. By the time a top-down project makes it to the coastal flood plain, it is likely that the area has been choked with *A. donax*, is badly degraded and the costs of control have greatly increased.

A more productive management strategy would be to work "inside-out." Under this strategy, treatments would be conducted within the flood zone first and then later in sites outside the flood zone. This would allow control activities to be concentrated in areas where *A. donax* is expanding quickly, and sites with fast-expanding plants should always be given the highest priority (Moody and Mack 1988). A second aspect of the "inside-out" strategy is that treatments should be started wherever *A. donax* is expanding quickly and this could be along any reach regardless of its position within a watershed, i.e., whether at the top, middle or bottom of the watershed. Biologists need to examine their watersheds and identify sites that look like Years 2 and 4 illustrated in Fig. 4 because these are sites where rapid spread is occurring or is imminent (cf. "nascent foci" of Moody and Mack 1988). Treating these sites first will prevent the rapid expansion of *A. donax* and reduce overall costs. The restoration sites can be anywhere in the watershed because the threat of reinvasion by fragments is relatively low. It is also worth noting that when *A. donax* recruits into a site – whether via fragments (Quinn and Holt 2003) or layers (personal observation; Fig. 4) – it does so mainly into open areas and does not easily invade closed canopies. Controlling *A. donax* and restoring native vegetation in the flood zone will tend to close the canopy and reduce the likelihood of future establishment of *A. donax* in that site.

Unfortunately, managers have been prioritizing sites on incomplete information about the way *A. donax* spreads and valuable resources have been wasted treating slowly expanding clumps in the upper reaches of watersheds. With an "inside-out" strategy managers can focus their resources in places where they will be most effective in reducing the spread of *A. donax*.

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SEED PRODUCTION BY THE NON-NATIVE *BRASSICA TOURNEFORTII* (SAHARA MUSTARD) ALONG DESERT ROADSIDES

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ABSTRACT

Plant biomass and seed production were quantified for *Brassica tournefortii* Gouan, Brassicaceae (Sahara mustard) from 3 sites spanning the Mojave and Sonoran deserts, in the Southwestern United States. We found strong linear relationships between plant biomass and seed production, with larger plants producing more seeds per plant ($R^2 = 0.93$) and greater seed biomass per plant ($R^2 = 0.94$). Both seed count ($R^2 = 0.93$) and seed biomass ($R^2 = 0.90$) were also greater in 0.25 m^2 plots that had higher plant biomass. These results and the law of constant final yield indicate that biomass and seed production of individual Sahara mustard plants can be higher in plots with lower densities. These data suggest that control efforts that do not remove all individuals may reduce densities but inadvertently increase net seed production within treated areas.

Key Words: Brassicaceae, disturbance, exotic, invasive, Mojave Desert, Sonoran Desert, *Brassica tournefortii*.

Brassica tournefortii Gouan (Brassicaceae [Sahara mustard]) was first recognized in Coachella Valley, California in the 1920s, and has since spread into cismontane California and throughout the Mojave and Sonoran deserts of North America (Minnich and Sanders 2000). It is regarded as one of the most invasive wildland pest plants in California (CalEPPC 1999; Cal-IPC 2005), and is being considered for addition to the Arizona noxious weed list (Ed Northam personal communication) and the Nevada noxious weed list (Dawn Rafferty personal communication). Sahara mustard is also one of the primary species targeted for control by land managers participating in the Mojave Weed Management Area in California and the Clark County Cooperative Weed Management Area in southern Nevada. Other land management units actively managing this species in the Mojave Desert include Lake Mead National Recreation Area, Joshua Tree National Park, and the Las Vegas Field Office of the Bureau of Land Management. It is also an identified management concern in the Sonoran Desert at Organ Pipe Cactus National Monument, Saguaro National Park (Sue Rutman personal communication) and the Coachella Valley National Wildlife Refuge (Cameron Barrows and Todd Stefanic personal communications), and on the Colorado Plateau at Grand Canyon National Park (Mary Zylo personal communication).

Since its introduction from the semi-arid and arid deserts of North Africa, the Middle East, and the Mediterranean regions of southern Europe, Sahara mustard has spread through the southwestern deserts of North America and is most common on roadsides, abandoned fields, and sand dunes (Minnich and Sanders 2000; Malusa et al. 2003). Roadsides offer increased soil moisture compared to the surrounding landscape, as they collect surface runoff from adjacent wildland areas during rains (Johnson et al. 1975; Vasek et al. 1975; Brooks and Lair accepted). Another advantage Sahara mustard has in establishing along roads is the formation of a sticky gel coat on seeds when they become wet, which allows seeds to adhere to vehicles (Minnich and Sanders 2000) and spread along roadsides.

Sahara mustard poses several threats to native desert vegetation. First, it has an early phenology giving it a head start over many native annual plants in utilizing soil moisture and mineral nutrients. The Mojave and Sonoran Deserts receive winter rain and annual plants typically germinate in response to rainfall events in fall and winter and bloom in early spring. Sahara mustard plants can flower as early as December, set seed as early as January, and most plants are fruiting or dead by April (Minnich and Sanders 2000; M. Brooks and J. Draper personal observations). Sahara mustard can complete its life cycle well before native plants have fully developed and reproduced (J. Holt et al. unpublished data; M. Brooks personal observations). The Sonoran Desert also receives summer monsoonal rainfall which can stimulate germination of Sahara mustard (M. Brooks personal observations), although its phenological timing in relationship to native summer annuals has not been reported. Second, Sahara mustard has the potential to create a continuous fuel load in areas where fuels

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are otherwise scarce and fires are infrequent. Historically, fires in Mojave and Sonoran Desert shrublands were infrequent due to low fuel loads between shrubs, preventing fires from spreading beyond ignition points (Brooks and Pyke 2001). The addition of extra fuel (Sahara mustard) could increase fire return intervals and many native desert species are not adapted to fire and their populations generally take much longer than non-native species to reestablish following fire (Brooks and Minnich 2006).

Desert annual plants are often referred to as ephemerals because they grow in habitats with unpredictable or infrequent resources such as precipitation (Barbour et al. 1999). Sahara mustard populations survive periods of summer drought as dormant seeds. During this life-history stage individuals are susceptible to predation from granivores and mortality from disease. The more seeds that can be produced, the safer the population is from depletion due to predation or disease before the next germination event. Seeds are also the singular unit of propagule dispersal for Sahara mustard, either when they are still within siliques attached to stem fragments and blown by wind, or after they are harvested by granivores (M. Brooks personal observation). As a result, producing more seeds means the population has a greater potential for persistence and expansion.

Efforts to control invasive annual plants such as Sahara mustard should ideally be designed to reduce inputs to the seed bank. Although removing individuals from a cohort may reduce their immediate effects on other plant species, the competitive release that can follow thinnings e.g., (Brooks 2000) may benefit remaining Sahara mustard plants. Thus, control efforts that only reduce density of Sahara mustard and do not completely remove all reproductive individuals may inadvertently increase growth and reproductive output of any Sahara mustard plants that remain.

Effective management of Sahara mustard requires knowledge of seed production and seed bank dynamics. In this paper we report patterns of seed production in Sahara mustard from the Mojave and Sonoran deserts of southwestern North America. We report seed production per individual plant and per unit area, and specifically evaluate the relationships of seed count and biomass with plant density and biomass. We focus on roadside populations, because this is where most control efforts to stop the spread of this species occur.

Methods

Sites were located in three areas in the Mojave and Sonoran deserts of California and Arizona, near the area where Sahara mustard was first collected and in the paths of its spread southeast and northeast into these deserts. The two criteria in choosing sites were that Sahara mustard be present along a paved road and in the adjacent wildland area, and that there be minimal disturbance at the site with the exception of the road itself. The three sites were located in: Coachella Valley, California along Interstate Highway 10, which is near the initial point of colonization for this species in North America (Minnich and Sanders 2000); Mohawk Dunes, located off of Interstate Highway 8 east of Yuma, Arizona; and along California State Highway 95 south of Needles, CA. Soils ranged from sandy at the Mohawk Dunes site to loamy and rocky at the Coachella Valley and Needles sites.

We sampled two microhabitats to include variation in plant production at two extremes of an environmental gradient, and two habitats to represent conditions typical of roadsides. The two microhabitats were: 1) beneath canopy–under the canopy of *Larrea tridentata* (DC.) Cov. (Zygophyllaceae [Creosote Bush]) or *Ambrosia dumosa* (A. Gray) Payne (Asteraceae [White Bursage]) shrubs; and 2) interspace–the area between shrubs that receives no shade from shrubs. The two habitats were: 1) along the roadside berm; and 2) greater than 20 m from the berm. Two replicate 0.25 m^2 plots were located within each of the two microhabitats within each of the two habitats at each of three sites, resulting in a total of 24 sampling plots.

Plants were collected soon after the foliage senesced in May 2003. Sahara mustard plants rooted within the boundaries of each 0.25 m^2 plot were carefully uprooted, the taproot was clipped directly below the rosette, and the samples were stored in paper bags until processing.

Above-ground plant density and biomass, and seed density and biomass, of Sahara mustard were measured for each sample. Plant density was defined as the number of plants rooted within each plot, and was reported to the nearest whole number. Plant biomass was determined by weighing plants prior to seed removal (to count the seeds) using an analytical balance (0.001 g precision), and reported to the nearest 0.01 g. Plants were individually weighed after they were air dried in a warehouse for 3 mo (May–July). Final dry biomass values were modified by subtracting the moisture mass, calculated using the average relative humidity of the storage space during the last month of drying (32.39%). We acknowledge this is a non-standard technique for determining dry biomass values, but we did not want to subject the seeds to oven heating since the seeds were to be used in subsequent germination and physiology studies. Seed density was determined by counting the number of seeds per plant, and reported to the nearest whole number. Seed biomass per plant was measured by collectively weighing all seeds removed from

TABLE 1. DENSITY AND BIOMASS OF SAHARA MUSTARD PLANTS AND SEEDS REPORTED AS AVERAGES (RANGE) FOR INDIVIDUAL PLANTS AND 0.25 m^2 PLOTS.

	Per Plant (n = 135)	Per Plot (n = 24)
Plant Density	n.a.	6 (1–23)
Plant Biomass (g)	4.07 (0.04–61.11)	22.92 (1.59–69.20)
Seed Count	995.75 (0–16,554)	5,601 (344–16,760)
Seed Biomass (g)	1.17 (0.00–19.05)	6.57 (0.47–21.44)

a plant, and reported to the nearest 0.01 g. Seeds were counted and weighed only if they were mature and viable. Viability was determined based on seed shape and color; seeds that were round and rust colored were considered viable as opposed to seeds that were flat or crushed and black. These guidelines to identify viable seeds were substantiated by subsequent germination tests (J. Holt et al. unpublished data).

Preliminary analyses indicated that there were no significant effects of microhabitat, habitat, or their interactions on seed production (count and biomass) at the individual or plot level. Seed production did vary significantly among sites ($P>0.05$), but the interactions of site with microhabitat and habitat were not significant. We therefore pooled the data into single analyses, using linear regression to evaluate relationships between plant characteristics (density and biomass) and seed production. We log-transformed the seed count data in order to normalize its distribution.

RESULTS

A total of 135 Sahara mustard plants were collected within the 24 plots. Mean above-ground dry biomass ($\pm$1 SE) of individual Sahara mustard plants was 4.07 $\pm$ 0.81 g, but ranged widely from 0.04 to 61.11 g (Table 1). Above-ground biomass per plot (0.25 m^2) averaged 22.92 $\pm$ 3.90 g (916,800 kg ha^{-1}; 818,585 lbs $acre^{-1}$). Density of standing plants per plot averaged 6 $\pm$ 1 plants (225,200 ha^{-1}), ranging from 1 (40,000 ha^{-1}) to 23 (920,000 ha^{-1}).

Seed counts for individual Sahara mustard plants averaged 996 $\pm$ 222 seeds, ranging from 0 to 16,554 seeds (Table 1). Seed counts per plot averaged 5,601 $\pm$ 1079 seeds (224,043,200 ha^{-1}). Total seed biomass for individual plants averaged 1.17 $\pm$ 0.27 g . Seed weights per plot averaged 6.57 $\pm$ 1.36 g (262,800 kg ha^{-1}). Of 135 plants analyzed, 11 weighed more than 10 grams and produced more than 2000 seeds, 46 plants weighed between 1 and 10 grams and produced between 300 and 2000 seeds, and 78 plants weighed less than 1 gram and produced less than 300 seeds per plant (Fig. 1a).

Larger plants produced more seeds and more total seed biomass than smaller plants. Seed count (Fig. 1a; seed count = 267(plant weight) - 90, R^2 = 0.95) and seed biomass (Fig. 1b; seed biomass = 0.32(plant weight) - 0.14, R^2 = 0.94) were both strongly related with plant size across the range of plants sampled. The size of individual seeds was also consistent across the range of plant sizes analyzed, as indicated by the strong linear relationship between seed count and seed biomass per plant (seed count = 0.22(seed biomass) - 0.15, R^2 = 0.94) (data not shown).

Seed production was highest on plots with the highest standing plant biomass. Seed count (Fig. 2a; seed count = 268(plant biomass) - 530, R^2 = 0.93) and seed biomass (Fig. 2b; seed biomass = 0.33(plant biomass) - 1.00, R^2 = 0.90) were strongly related to biomass of Sahara mustard plants per 0.25 m^2 plot. These results follow from the positive linear relationships of seed count and seed biomass per plant with plant size (Fig. 1a, b).

Although not statistically significant, seed count and biomass were lower in plots with the highest Sahara mustard densities (Fig. 3a, b).

DISCUSSION

Some individual Sahara mustard plants produced > 16,000 seeds in this study. However, the largest plants in our data set were only approximately 50% the size of many of the largest individuals found in the field during years of especially high rainfall and thus the largest individuals may produce substantially more seeds (M. Brooks, personal observation). The Sahara mustard plants used in this study were collected in 2003, a year that received below-average rainfall (Table 2). 2004 and 2005 were years of higher-than-average rainfall and Sahara mustard plants in these years were noticeably larger than in 2003.

Other weedy plants occurring in the Mojave Desert have been reported to produce widely variable numbers of seeds. Two plants in the Brassicaceae family, *Brassica nigra* (L.) Koch and *Sisymbrium altissimum* L., reportedly produce 13,400 and 80,400 seeds per plant, respectively (Stevens 1932). Russian thistle or tumbleweed (*Salsola tragus* L.) can produce 24,700 seeds per plant (Stevens 1932). A non-native annual grass common in the Mojave Desert, *Bromus madritensis* L. subsp. *rubens* (L.) Husnot, reportedly produces 446 to 575 seeds per plant (Huxman et al. 1999). *Chenopodium album* L., a weedy annual forb has been recorded as producing anywhere from 31,000 (Salisbury 1978) to 72,450 (Stevens 1932) seeds per plant

We know from the law of constant final yield (Kira et al. 1953; Hozumi et al. 1956) that as plant densities increase, plant size and seed production per plant decrease in response to

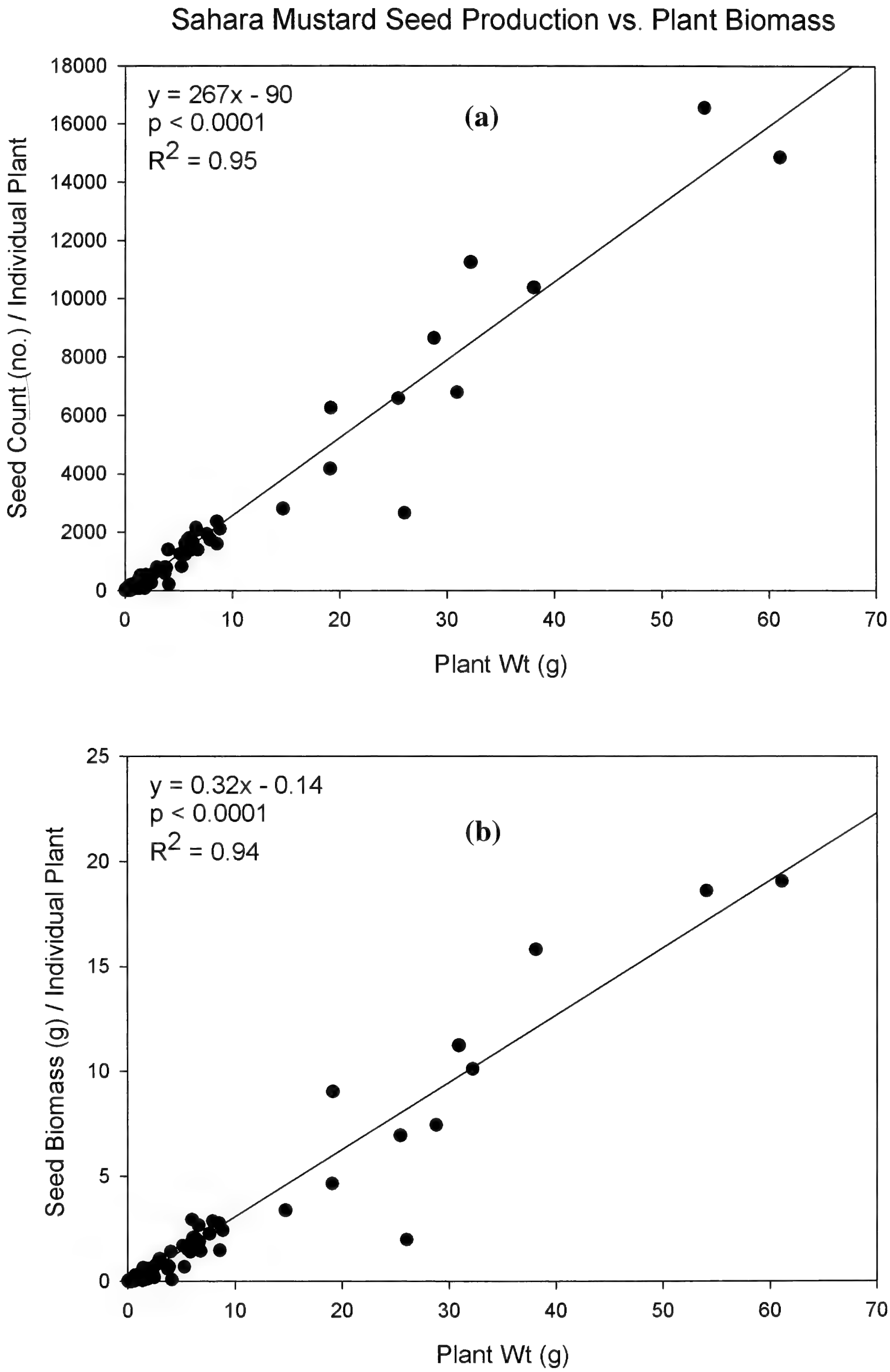

FIG. 1. **(a)** Linear correlation of seed count related to biomass per individual plant. **(b)** Linear correlation of seed biomass related to biomass per individual plant.

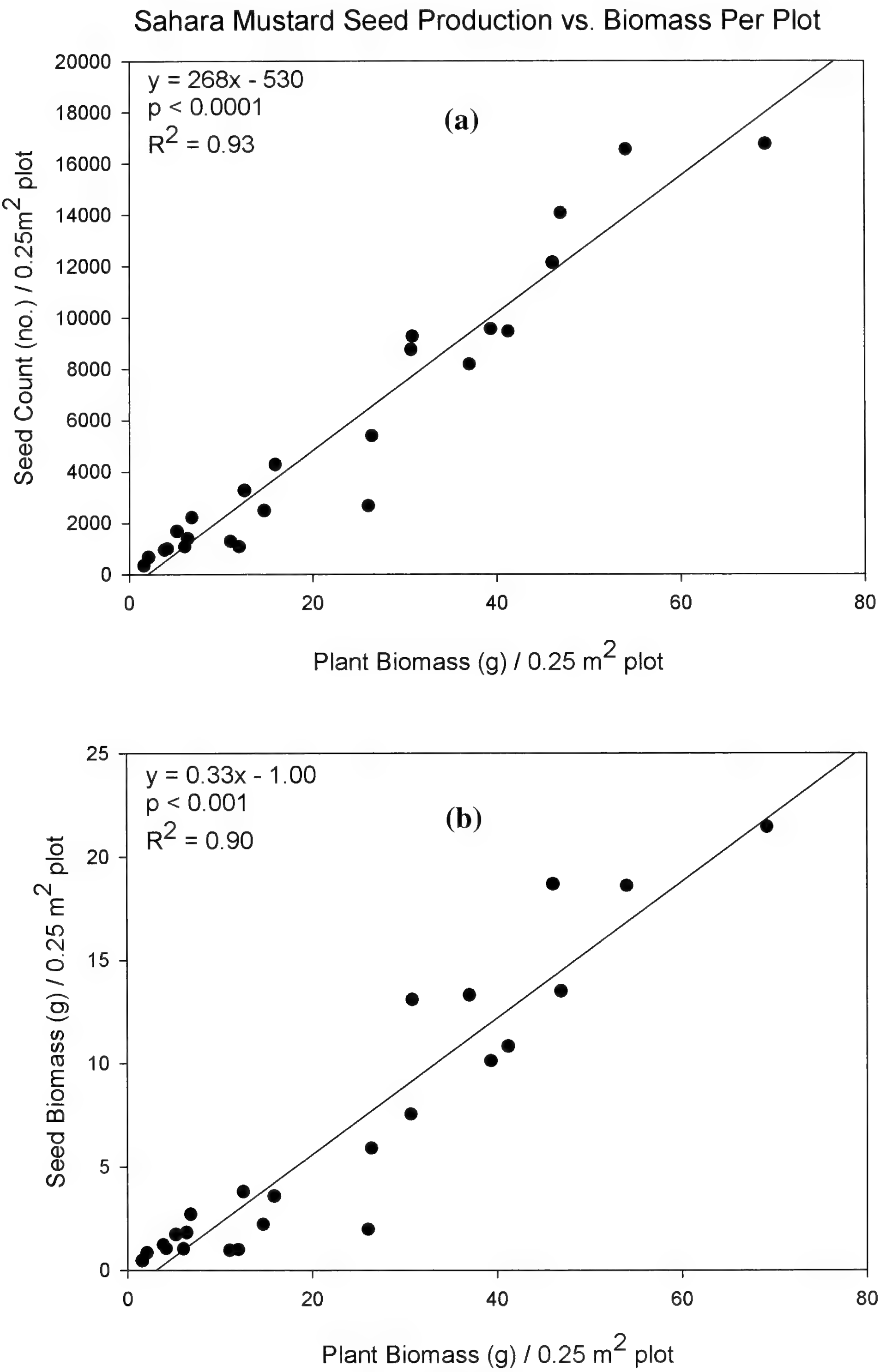

FIG. 2. **(a)** Linear correlation of seed count related to plant biomass per 0.25 m^2 plot. **(b)** Linear correlation of seed biomass related to plant biomass per 0.25 m^2 plot.

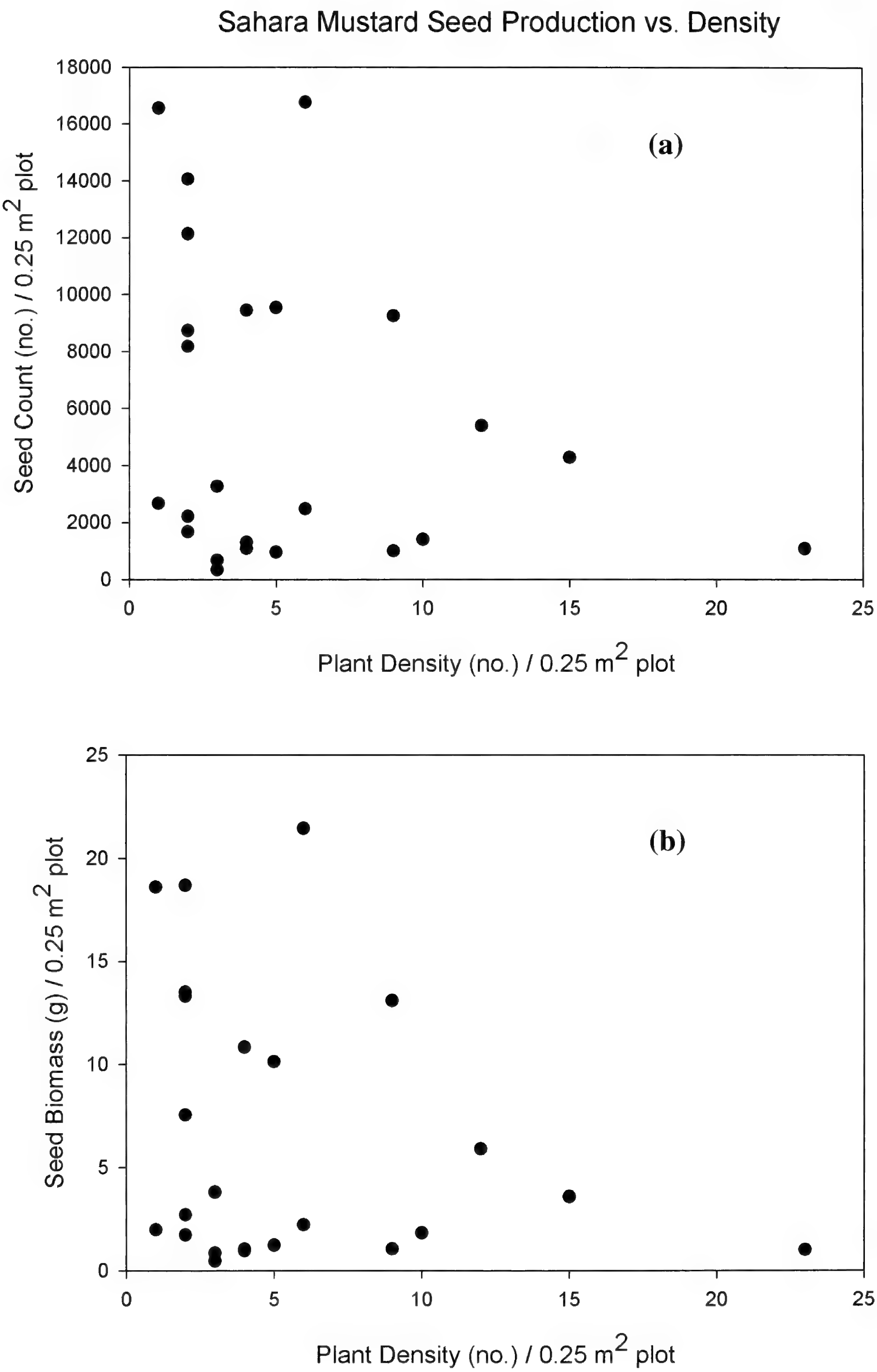

FIG. 3. **(a)** Scatter plot of seed count values related to plant density within a 0.25 m^2 plot. **(b)** Scatter plot of seed biomass values related to plant density within a 0.25 m^2 plot.

TABLE 2. PRECIPITATION AND DEPARTURE FROM NORMAL PRECIPITATION (CM) AT THREE WEATHER STATIONS NEAR THE NEEDLES, COACHELLA VALLEY, AND MOHAWK DUNES STUDY SITES (U.S. DEPT. OF COMMERCE 2003, 2004, 2005). * At time of preparation, only January–August 2005 precipitation data was available online.

Weather station	2003		2004		2005*	
	Precipitation (cm)	Departure (cm)	Precipitation (cm)	Departure (cm)	Precipitation (cm)	Departure (cm)
Needles AP	11.58	−1.40	16.08	3.10	12.95	4.29
Palm Springs	12.42	missing	19.86	missing	18.54	8.81
Yuma Proving Ground	9.14	−0.51	18.44	8.79	13.41	7.39

limiting resources and increased competition. Mean plant size and rates of emergence have been found to be negatively correlated with initial seed density in annual plant communities (Lortie and Turkington 2002). Species that have been recorded as producing fewer seeds at increased densities in the Mojave Desert include *Bromus madritensis* L. subsp. *rubens* (L.) Husnot (Harper 1961; DeFalco et al. 2003), *Vulpia octoflora* (Walter) Rydb., and *Descurainia pinnata* (Walter) Britton (DeFalco et. al. 2003), *Conyza canadensis* (L.) Cronq. (Palmblad 1968), *Pectocarya recurvata* I. M. Johnston, and *Plantago patagonica* Jacq. (Pantastico-Caldas and Venable 1993). Although not significant, the four plots in our study with the highest Sahara mustard densities had lower seed production than many plots with lower Sahara mustard densities.

The preliminary results mentioned in the Methods section indicate that microhabitat (beneath shrub canopy and interspaces between shrubs) and habitat (roadside and off-road) did not significantly affect seed production, but we believe this lack of significance to result from differences in soils at the three study sites. The Mohawk Dunes site has sandy soils which Sahara mustard prefers (Minnich and Sanders 2000), and can often dominate irregardless of other factors such as localized conditions created by shrubs and roads (Brooks accepted, M. Brooks personal observations). The soils at Needles and Coachella Valley are loamy and rocky, which Sahara mustard does generally not prefer, and where shrubs and roads can have a much stronger effect on dominance of this species (Brooks accepted). Variation in microhabitat and habitat effects among the three sites was one of the reasons for lack of statistical significance of these variables. Additional sites, replicates, and stratification of soils are needed to strengthen these ideas about Sahara mustard's habitat and microhabitat preferences.

MANAGEMENT IMPLICATIONS

Seed production should be considered when implementing control efforts and when creating effective follow-up strategies for any annual plant species, including Sahara mustard. The law of constant final yield and the results of this study suggests that plots that are only thinned during control efforts for Sahara mustard, leaving some individuals alive (e.g., hand-pulling or spraying a site once and not returning to look for survivors), may not reduce seed production and could inadvertently produce more standing biomass and have higher seed production than plots that are left untreated. The net result may be a more plentiful seed bank than would have existed if the smaller, less productive plants were left in place. Although this hypothesis remains to be tested, it suggests the importance of destroying all plants in a target area when control efforts are employed. This may require resurveys and follow-up treatments during the remainder of the growing season to locate and destroy plants that were missed the first time and to remove plants that have emerged since the initial treatments. Second and even third cohorts of Sahara mustard have been observed within the same growing season in the Mojave Desert (M. Brooks and M. Trader personal observations). Managers should be aware that this plant can produce several germination cohorts per year and that additional treatments may be required to remove all cohorts, as well as those which survived previous control treatments. It is therefore advisable to focus control efforts on repeated treatment and monitoring of smaller areas, than single treatments of larger areas.

As stated in the introduction, Sahara mustard poses threats to native desert vegetation. Currently, little information about this plant exists in the literature and additional research is necessary to create effective management plans. Information related to seed banks is specifically needed to evaluate Sahara mustard seed bank dynamics, seed longevity and persistence in soil, and the effects of plant density, microhabitats, and roads on seed production.

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BIOLOGY OF THE GEOPHYTIC LILY, *TRITELEIA LAXA* (THEMIDACEAE), IN GRASSLANDS OF THE NORTHERN SACRAMENTO VALLEY

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ABSTRACT

Triteleia laxa (Themidaceae), a liliaceous geophyte common in California at lower elevations with mediterranean climate, was studied during 1998–2004 at four sites in the northern Sacramento Valley. New individual plants were randomly selected each year at one to four of these grassland or open savanna sites to provide a composite study of the biology and life history of the plant. A mature plant produced two leaves after fall rains begin, a new corm on top of the shrinking old corm in spring, and a scape with an umbel of large bluish flowers in late March or April. By seed production in May, above-ground parts were dead, and the new corm and seeds persisted through summer. Mean leaf lengths varied from 22 to 28 cm; no correlation was found with amount of precipitation. Mean scape lengths also varied, from 23 to 32 cm; overall, there was a negative correlation with spring precipitation. Corms of flowering plants had a mean volume of 1.30 cm^3, and occurred at a mean depth of 7.27 cm; corm volume was correlated with scape height and with number of flowers. Dry mass increased linearly in the new corm during the spring growth period. Number of flowers per plant varied among sites and the mean varied highly significantly among 5 yr (range 8–12.6). Plants appeared to be largely self-incompatible, but produced a small number of selfed seeds when pollinated by hand. The pollen:ovule ratio was about 3100:1. Mean fruit set (range 50–74%) and mean seed set (range 40–58%) were low, and varied significantly among sites and years. Seed mass averaged about 1.7 mg, and seeds showed 100% viability. Germination time was about 4 wk after wetting, with up to 98% of seeds germinating. The seedling was carried downward from the seed by the elongating cotyledon, ultimately producing a single foliage leaf, a lateral contractile root that shortened in April (and *in situ* doubtless pulls the seedling deeper into the soil), and a corm <4 mm in diameter. Soils occupied in study sites were loams, with 20 to 39% clay particles. This study on *T. laxa* gives a reasonably complete picture of the biology for a common geophyte, and we hope that this work will provide impetus for additional studies of other widespread or local geophytes.

Key Words: *Triteleia laxa*, geophyte, mediterranean climate, annual grassland, corm, contractile root, low fruit and seed set.

Geophytes are perennial herbs that survive unfavorable periods for growth by dying back to underground storage organs such as corms, bulbs, tubers, or rhizomes (Rundel 1996). Dafni et al. (1981) have categorized geophytes as either "synanthous" (leaves and flowers produced in the same season) or "hysteranthous" (leaves and flowers appearing in separate seasons). Dafni et al. also point out that the underground storage organs of these perennial geophytes can be "annual" (that is, the old storage organ is completely replaced by a new organ each growing season) or perennial (with tissue added to the same organ over the years). In the two-season mediterranean climate, geophytes commonly dry up and become dormant aboveground during the dry summer and then renew growth from the storage organ when water becomes available during autumn, winter and spring (Rundel 1996; Parsons 2000). Thus, these geophytic species follow a phenological pattern similar to that of most annual herbaceous species (which persist as seeds during summer) in California's savannas and grasslands (see especially Chiarello 1989).

The early, classic study of plant life forms (Raunkiaer 1934) noted that geophytes were well represented in areas with mediterranean climate. In (largely mediterranean) California, monocotyledonous geophytes constitute about 5% of native vascular plant species (Rundel 1996). Recent studies are still cataloging and making numerical comparisons of geophytic species occurring within different regions with this climate (Poches and Cowling 2004; Poches et al. 2005; Parsons 2000; Parsons and Hopper 2003). For geophytes of western Australia and some other regions with mediterranean climate, Pate and Dixon (1982) have provided detailed information on the morphology and anatomy of corms, bulbs and tubers, as well as on growth and phenology. There is a paucity of this type of information for California's geophytes. For example, no information on geophytes is in the book "California Annual Grasslands" (Huenneke and Mooney 1989).

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Many monocotyledonous geophytes of the "lily type" (Liliaceae *sensu lato*, as in Hickman 1993; FNAEC 2003) grow in grasslands and savannas of the northern Sacramento Valley of California and include species of *Calochortus*, *Chlorogalum*, *Fritillaria*, *Odontostomum*, *Zigadenus*, *Allium*, *Brodiaea*, *Dichelostemma*, and *Triteleia*. (*Triteleia* and several others of these genera are currently placed in families other than Liliaceae [e.g., see Pires and Sytsma 2002; FNAEC 2003].)

Several of the geophytic species that grow in California's low elevation grasslands have had limited information on features characterizing or affecting portions their of life cycles (in these grasslands or elsewhere) published or presented in dissertations and theses. For example, reproduction and corm size in *Zigadenus fremontii* (Torrey) S. Watson was studied in relation to fire in southern California (Tyler and Borchert 2002), and its reproduction and survival have been studied in the northern Sacramento Valley (Mitchelson 1993). For *Calochortus luteus* Lindley, there are descriptions on floral phenology, pollen:ovule ratios and insect flower visitors/ pollinators (Jokerst 1981), features of the pollen grains (Kannely 2003), and aspects of pollination in relation to evolution in the genus (Dilley et al. 2000). In *Chlorogalum angustifolium* Kellogg, floral biology was studied by Jernstedt (1982), and the same author (Jernstedt 1984) published considerable detail on seed germination and the development of seedlings' contractile roots in *C. pomeridianum* (DC.) Kunth. Jernstedt (1980) also studied flower development and anthesis in *C. pomeridianum*, and Stockhouse and Wells (1978) presented information on pollination in this species. *Brodiaea californica* Lindley has had flower phenology, flower visitors, and seed production documented by Doalson (1999). *Triteleia hyacinthina* (Lindley) E. Greene has had seedling development described by Smith (1930) and Putz (1992), and much earlier, *Dichelostemma pulchella* (Salisb.) E. Greene and several other geophytes had seedling development described (Rimbach 1902). *Fritillaria pluriflora* Benth. has had low fruit- and seed set described by Witzman (1991). There is some basic life cycle information included in the mainly taxonomic papers for members of *Brodiaea*, *Dichelostemma* and *Triteleia* by Keator (1987, 1989) and Niehaus (1980), and especially in the biosystematic study of *Brodiaea* by Niehaus (1971). Keator (1967) has amassed considerable information from field and garden studies for six species of *Dichelostemma* (e.g., on phenology, corms, flowering, seed production, and germination), but most of this work is unpublished. Despite all these studies for geophytic species that can be found in the area of the present study, we and others (Rundel 1996; Parsons 2000) believe that life cycle biology and natural history in the field is incompletely known for geophytes in California.

To augment the sparse literature on California geophytes, *Triteleia laxa* Bentham was chosen for study. *Triteleia*, a mainly Californian genus, is composed of 15 species, all of which occur west of the Rocky Mountains (FNAEC 2003). *Triteleia laxa* (commonly called Ithuriel's Spear, Grass Nut or Walley Basket) is a synanthous geophyte occurring in the region with mediterranean climate in Western North America, ranging from San Bernardino County, California to Currey County, Oregon (Hoover 1941; Munz and Keck 1959; Keator 1993). This widespread species is found from sea level to 1500 m in elevation (Keator 1993), less commonly in open forest and chaparral, but more commonly in low elevation savanna and grassland ecosystems.

In *T. laxa*, the perennating corm first produces two long, grasslike leaves during the cool and rainy mediterranean winter season, and then a single scape 10–70 cm tall, bearing an umbel of large bluish trumpet-shaped flowers in the spring as the rainy season ends. After fruit and seed production, and formation of a new corm on top of the old corm, leaves and scape dry up, and aboveground activity ceases during the hot, dry summer months. With the fall rains, the corm initiates root growth and seed germination also occurs.

Triteleia laxa plants are notable for their morphological variability, as in height and in size and color of flowers (Hoover 1941; Keator 1993). The time of flowering also varies, with more-coastal variants flowering several months later than elsewhere (Hoover 1941). Corms of some variants have been successfully introduced into the horticultural trade, and are often listed in popular gardening catalogs.

Several environmental conditions of importance in the horticultural mass production of *T. laxa* for commerce, e.g., those promoting seed germination and cormel (vegetative corm) production, have been studied, but only in gardens and in laboratory experiments (e.g., Fortanier 1969; Han 1993; Han and Halevy 1993; Han et al. 1991). Anatomical development of the ovule, embryo sac, and endosperm has been described (Berg 2003), and polyploidy has been documented (n = 7, 8, 14, 16, 21, 24) among wild-collected populations (Lenz 1966; Davidson 1975; Keator 1993). According to Han (1993), this species is self-incompatible, requiring pollen transfer between plants for seed production.

However, there are very few details published about this plant's biology where it is growing in the wild. Field studies of this plant are particularly warranted because it represents one of the most common geophytes of lowland mediterranean California. Its corms are almost certainly an important food source (e.g., Anderson and

Rowney 1998) that may be used by rodents and other animals. It also represents a large pollen and nectar food-source for insects.

The purpose of our study is to document aspects of the biology and ecology for *Triteleia laxa* in the northern Sacramento Valley. We provide basic information on three topics: 1) phenology and growth of leaves, scapes, and corms; 2) features of sexual reproduction; and 3) features of the seed and seedling stages in the life cycle.

Study Areas

Areas with high densities of *Triteleia* were chosen for study near Chico, California, in the northern Sacramento Valley. The main study area, utilized 1998 through 2004 and referred to as "Vina" below, is located about 16 km north of Chico, east of Cana Pine Creek Road in extreme northern Butte County (39°52′46.6″N, 121°58′34.5″W), at the Vina Plains Preserve (owned and managed by the California Nature Conservancy). Grassland covers the gently rolling terrain of this preserve. This region is underlain with cemented materials of volcanic mudflow origin, washed down historically from the Tuscan Formation of the southern Cascade Range to the east (Broyles 1983, 1987). The soils are usually less than 1 m deep on top of this cemented hardpan (Gowans 1967). Soils where *Triteleia* is most abundant are clay loams, with clay particles ranging from 33–39% of total soil particles, according to analysis by A. & L. Western Agricultural Laboratories, Modesto, CA. These soils will be classified as part of the Tuscan Series in the "Butte Area Soil Survey" being completed by the Natural Resources Conservation Service (Andrew Conlin, pers. comm.). These grasslands contain about 275 species of vascular plants, with about one third of these being exotic species (Broyles 1987; Mitchelson 1993; Oswald 1997). This main Vina site, at 52 m in elevation, had not been grazed by cattle since the study began in the spring of 1998 (Oswald 1997), although cattle were present for several weeks in April of 2003. The area was control-burned in early June 1997, the year before field study began, and again in 1998, 2002, and 2003; in each case, this was after the *Triteleia* growing season was over.

In 1998, 1999, and 2000, a second population of *Triteleia* was studied in the Preserve, about 2.3 km east of the main Vina study area, and east of Hwy 99 in southern-most Tehama County (39°53′38.6″N, 121°58′34.5″W). This site (referred to as "Barn"), at 62 m in elevation, has soils similar to those of the main Vina site. The region was control-burned in 1998, after the first year of study, and cattle grazed here several of the winter months each year of the study.

In 2003 and 2004, a "Park" study area was added, within Bidwell Park, on the east side of Chico (39°46′42.8″N, 121°45′10.8″W) at about 99 m in elevation. The *Triteleia* population here grows on a heavy loam of an ancient alluvial terrace above Chico Creek (Red Bluff gravelly loam), with about 25% clay particles (Andrew Conlin, pers. comm.). Vegetation is savanna, with a sparse overstory of *Quercus douglasii*. Neither burning nor grazing by cattle occurred immediately preceding or during the study years.

In 2003 and 2004, a "Road" study area was also utilized, just to the east of Chico along Humboldt Road (39°44′58.8″N, 121°45′10.8″W) at 131 m in elevation. Soils are derived from Tuscan Formation volcanic mudflows, and are gravelly loams with about 20% clay particles, classified as Typic Haploxeralfs (Andrew Conlin, pers. comm.). Vegetation is savanna, with a sparse overstory of *Quercus douglasii*. Neither burning nor grazing by cattle occurred immediately preceding or during the study years.

The climate at all sites is typical mediterranean, with cool, wet, winters alternating with hot, dry summers. Most (86%) precipitation (mean 55.5 cm) occurs as rain from November through April (Fig. 1; NOAA 2005).

Methods

Sampling

Transects were established subjectively to cross through areas of abundant *Triteleia* plants. Two permanent 30–m transects were established at Vina, one mainly for observations on phenology and the other for measuring and/or destructive sampling of plant parts. Additional (temporary) transects were also set up at each study site for observations or for destructive sampling. For most aspects of study, plants were selected randomly on cross-transects (up to 6 m long) at right angles to the main transects every 1–2 m. Individual plants selected for whole-season observation had wire stakes with aluminum identification labels pushed into the soil 10 cm south of the plant base.

Phenology

Above-ground Shoots and Weather Data. Phenological measurements were made for 50–60 plants along a permanent 30-m transect at Vina for five years. Most plants selected for study could not be followed for more than one growing season due to the burrowing activities of pocket gophers (*Thomomys bottae*) dislodging the identification stakes and/or destroying the corms; thus, new individuals were chosen each season. In some cases gopher activity necessitated choosing

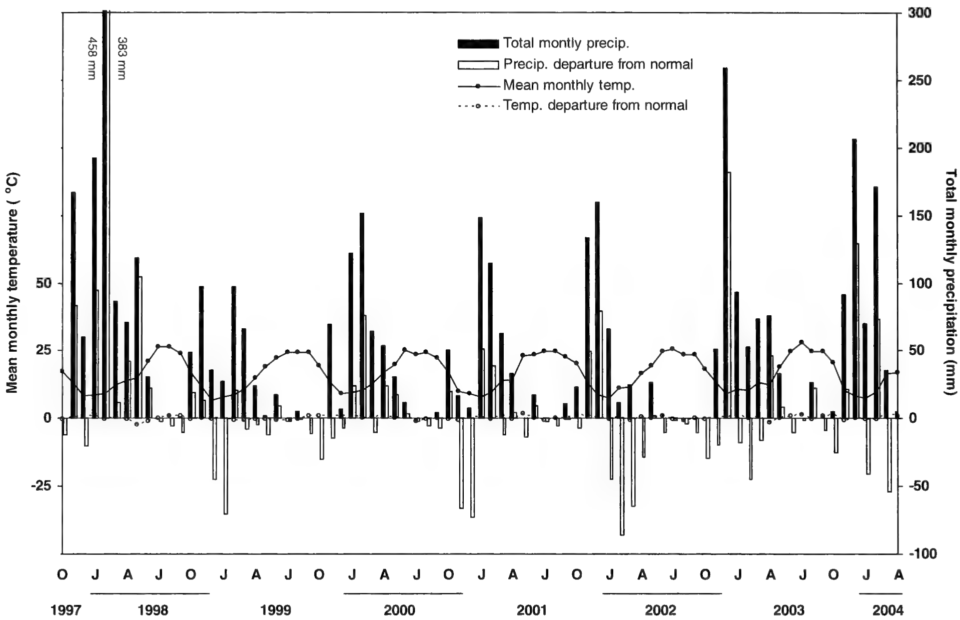

FIG. 1. Approximated mean monthly temperature and total monthly precipitation for the Vina and Barn study areas, from a weather station in Orland, CA from October 1997 through April 2004 (NOAA 2005). Mean monthly temperature and precipitation departure is the amount deviating from a 30-yr mean.

several new individuals to measure during a growing season.

Start time for measurement varied during the years of study, but usually began soon after emerging *Triteleia* leaves were recognizable at the soil surface in February. In 1999, start time began in late March, when leaves were already approaching maximum length. Frequency of observation was weekly in 1998. Leaves and scapes were measured every four days in 1999. Leaves were measured every two weeks, but scapes weekly in 2000. Both leaves and scapes were measured weekly in 2002, 2003, and 2004. Length of both leaves was measured to the nearest 0.5 cm, from ground surface to leaf tip. Emerging scapes were measured from ground surface to the tip until the developing inflorescence was apparent, after which the scape length (=height) was measured from ground surface to the base of the umbellate inflorescence.

Phenological measurements on leaf and scape growth at Vina were not started at the same time each year, but were carried out until the marked plants reached maximum scape height at flowering in each of five years. The number of plants on which leaf growth was measured started out at 50 to 60 new individuals each year, but was usually lower (16–44 individuals) by the time of flowering because 1) gophers (and possibly rabbits and mice) herbivorized plants or dislodged/toppled identifying stakes, and 2) some individuals were mis-identified (i.e., *Dichelostemma*, *Chlorogalum*, and *Calochortus* leaves look much like *Triteleia* leaves initially). Also, the number of scape measurements was lower on earlier dates because scapes did not start growth at the same time. Mean leaf length became *shorter* late in the growing season, because tips of the leaves shriveled and dried and broke off; thus, *maximum* leaf lengths were compared among the years.

Analysis of scape lengths was done only on four years (2000, 2002–2004), because data in 1999 could not be obtained randomly due to scapes dying before flowering. Leaf and scape length measurements were not made in 1998 or 2001.

Corms. In early March 1998, corms were excavated from randomly selected *Triteleia* plants commencing scape growth at Vina. Corm height and two diameters (widths) were measured with calipers to the nearest 0.5 cm, and corm volume was estimated as the volume of a sphere, based on the mean of the three measures. In latest April here, and also at the Barn site, additional corms were dug at randomly selected points, using pairs of the tallest and the closest, shortest flowering scapes, in order to determine if scape height, flower numbers, or soil depth of the corm was correlated with corm volume. All measurements were made with the corm coat still present.

In the growing season of 2002, random corms were excavated every two weeks at Vina to determine volume and mass. This time the corm coat was removed and the two parts of each corm (the plump, developing, new corm and the shrinking remains of the old mother corm producing the leaves and scape) were measured

separately. In December of 2004, non-randomly selected corms were dug at Vina to check volume and mass, and to determine extent of growth after the earliest rains of fall; again, the corm coat was removed and old and new parts were measured separately.

Breeding System and Pollination

At Vina in 1998, inflorescences were bagged with sheets of microscope lens tissue to exclude insect pollen vectors, and later examined for fruit and seed set. In 2000, individual flowers were bagged with strips of lens tissue for 48 or more hours. Bags were gently removed, and wooden toothpicks were used to transfer pollen in three types of pollinations within and between inflorescences: 1) pollen to stigma in same flower (autogamous), 2) pollen to stigma in separate flowers on same plant (geitonogamous), and 3) pollen to stigma in separate flowers on different plants (xenogamous). Treated flowers were re-bagged and examined for seed set in several weeks. Open-pollinated (marked, but not manipulated) flowers nearby were used as controls. At Vina in 2004, squares of tulle (a green net material with about 1 mm mesh) were gently tied around 30 inflorescences to exclude flower visitors; 30 nearby plants without tulle were marked to serve as controls. All flowers were examined for fruits and seeds in 2–3 wk.

To elucidate the period of stigmatic receptivity within individual flowers, a colorimetric assay was carried out at Park to test for the presence of stigmatic peroxidase enzymes. Four flower stages (n = 25 for each stage) were designated for the assay: a) flower buds nearly open (flowers collected), b) flowers recently opened (1–3 d old), c) flowers with anthers mostly dehisced and with the style bent towards the middle of the flower (2–4 d old), and d) flowers recently closed and most without any sign of seed formation yet (4–6 d old). Sampling was done between 2–4 pm (PDT) on 30 April 2003, and samples were placed in a freezer within twenty minutes of the last collection; the assay was carried out seven days after collection. Peroxidase activity was detected *in planta* with adoption of methods used by Blee et al. (2003).

Pollen/ovule ratios were determined for 35 plants in the Vina population on 31 March 1998. Large flower buds with indehisced anthers were collected into botanical FAA. In the lab, one anther per flower was stripped of pollen with a needle in a 4 dram vial containing 1 ml FAA or 1 ml water. After vigorous shaking, an aloquat in a dropper was quickly transferred to a hemocytometer and a volume of 0.04 ml solution had pollen grains counted; this number was multiplied to represent the number of grains dispersed throughout the entire volume of solution. Anthers from the upper and lower tiers were compared. Each flower that had pollen counted in one anther also had the ovules from the ovary counted under a dissecting scope. Pollen grains X 6 (6 anthers per flower) divided by the number of ovules gave the estimate of pollen:ovule ratio. Ratios were determined for each flower before being averaged.

In April 1998, unopened flower buds at Vina were bagged with strips of microscope lens tissue for 18 or more hours to provide samples of nectar. Nectar withdrawn from bagged flowers with 10 mu capillary pipettes had sucrose equivalents (SUE) determined in the field with a Bellingham and Stanley pocket refractometer on 17 April. A few flowers (despite the bagging) had thrips present in the corollas that may have contaminated nectar with pollen; samples with suspected contamination were not used to calculate mean SUE. The volume of nectar varied, and although all samples were from separate plants, in 11 of 28 plants more than one flower had to be used to obtain a volume large enough to register on the refractometer.

Reproductive Output: Flowers, Fruits and Seeds

To determine variation among plants in flower, fruit, and seed production, flowers per plant, fruits per plant, and seeds per fruit were counted at each site in several years. Counts were made when plants were in fruit; number of flowers produced was ascertained by adding number of fruits and empty pedicels remaining—the latter indicating abortion of either a flower or a young fruit. Seeds per fruit were determined for two dried, indehisced fruits from each randomly-selected inflorescence. In several years, a dissecting microscope was used to also count aborted ovules remaining in the dried fruit.

Seed Weight, Viability, and Germination

A collection of mature seeds from about 200 inflorescences in the Vina population was made on 1 June 1997. Seed lots were stored in an indoor laboratory at ambient temperature and in an uncooled/unheated garage, where summer and winter outdoor (=field) temperatures of Chico were approximated. Forty seeds from both indoor- and garage-stored lots were weighed individually, on a Sartorius analytical balance in March 1998.

In 2003, collections of mature seeds, each from 100 or more inflorescences, were made at Vina (22 May), and at the Park and Road sites (27 May). Seeds from each site were stored in a garage in Chico where summer and winter outdoor temperatures were approximated, until viability tests and outdoor germination tests were made.

Seeds from each site, stored under outdoor temperatures, were subjected to viability tests in December 2003. For each site, 50 "good" seeds (dark-colored and unwrinkled) were placed in a Petri dish, on filter paper wetted with distilled water, and kept at ambient temperature in a cupboard for 45 hr. The viability of each seed was then tested with tetrazolium-chloride adjusted to pH 6.5 (Baskin and Baskin 1998).

To evaluate the proportion of seeds germinating, when they germinated, and when the shoot reached the soil surface, seeds collected at Vina and stored under outdoor conditions in 2003 were planted in a garden plot in Chico with prevailing outdoor temperatures and only natural precipitation. On 30 November, in a raised garden box with sandy loam soil, seeds were planted 8–10 mm deep, in 10 rows of 50 seeds spaced 20 cm apart, on strips of moistened, non-inked newsprint paper 3 cm wide (so that recovery of germlings would be possible). The first row of germinating seeds was recovered in four weeks (28 December), and additional rows were exhumed every two weeks through 9 April 2004.

Climatic Data

Monthly climatic data for Orland, CA were used to approximate weather at the Vina study site, which is about 18.5 km northeast of Orland (NOAA 2005; Fig. 1). Daily measurements of precipitation, and minimum and maximum air temperatures at Orland and Chico were used with our phenological measurements and seed germination experiment, respectively (UCD 2005).

Data Analysis

Means for many traits measured (e.g., leaf length, scape length, flowers per plant) did not always have homogeneous variances, so non-parametric (Kruskal-Wallis, Dunnett T3, Tamhane or Games-Howell) analyses were used to test for differences in these cases. However, since we usually had large sample sizes, and the probabilities obtained from non-parametric tests were nearly identical to the P values obtained from ANOVA and Tukey HSD comparisons, we have usually reported the latter. Where its assumptions could be adequately satisfied, ANOVA followed by Tukey HSD comparisons was used to test differences. Repeated measures ANOVA was used to determine if scape growth rate during the logistic growth phase varied among years. Spearman's rho rank test was used to check for correlations. Most data analyses were preformed using SPSS software (Release 11.0.1, Chicago, IL), but some analyses were done using JMP IN 3.2.1 for Macintosh (SAS Institute, Inc., Cary, NC).

Results

Phenology and Growth of Aboveground Parts

Mean maximum leaf and scape lengths differed among some years (Table 1). There was not an association between precipitation and leaf length, based on precipitation of the entire winter-spring growing season (1 October to date of maximum length) or on precipitation occurring only in the days of the (warmer) study period starting in February (Figs. 2 and 3). There was, however, a highly significant ($P < 0.0001$) negative correlation ($r_s = -0.408$, $n = 153$) of maximum scape length with precipitation of the study period (1 February to date of maximum length).

Raw data on lengths from four comparable sample dates in the logistic phase of scape growth in 2000 and 2002–2004 indicated that there was a significant affect of year on scape growth rate. The highest growth rate, in 2002 (10.4 cm per week) was highly significantly greater ($P < 0.001$) than in all other years (Table 1). The lowest growth rate was 5.5 cm per week in 2004. In these four years, flowering occurred a few days after maximum scape length was reached.

Leaf lengths, but not scape lengths, for 1999 are included in Table 1, because the scapes died just before flowering. By 7 April, effects of an unknown pathogen were first noticed as a downward bending of the scape several cm from the top. In a few days, the inflorescence and portion of the scape above the bend died, leaving the unopened, or barely-opened flower cluster dangling (Fig. 4a). By 2 May, 33 (94.3%) of the original 35 marked plants producing scapes at Vina had dead non-fruiting scapes due to this disease. A similar effect was observed in the Barn population, with dead scapes on 26 (76.5%) of the original 34 plants producing scapes. Phenology was not studied in 2001, but the same scape death phenomenon was observed in both Vina and Barn populations.

Corms

Corm volume comparisons, and corm depths in the soil. Corm volume (mean ± SE) in cm^3, when first measured on 2 March 1998, at Vina, was 1.62 ± 0.131 ($n = 30$); all corms came from plants that had flowered the previous year. Paired corm volumes (longest and shortest flowering scapes) from Vina longest plants (1.76 ± 0.137; $n = 30$) and shortest plants (0.91 ± 0.059; $n = 30$) were highly significantly different ($P < 0.0001$) as were the paired corm volumes for Barn longest plants (1.56 ± 0.114; $n = 30$) and shortest plants (0.96 ± 0.080; $n = 30$). However, when long-plant corms from Vina and from Barn were compared, they did not differ significantly in volume, nor did the short-plant corms from the two sites ($P = 0.589$

TABLE 1. SUMMARY OF FIVE YEARS OF LEAF AND SCAPE PHENOLOGY FOR *TRITELEIA LAXA* AT A GRASSLAND SITE (VINA) IN THE NORTHERN SACRAMENTO VALLEY. See Figs. 2 and 3 for sample sizes. ANOVA and Tukey HSD comparisons were performed separately for leaf and scape lengths, and repeated measures ANOVA was performed for scape growth rate. Values within a column sharing the same superscripts are not significantly different. Leaf length differences are significant at $P < 0.025$ for 1999 vs. 2002 and 2003 vs. 2004, and $P < 0.001$ for 2002 vs. 2004. Scape length differences are significant at $P < 0.001$. Scape growth rate differences are significant at $P < 0.001$, except 2000 vs. 2003 at $P < 0.025$.

	Mean (±SE) maximum length (cm)		Date of maximum length		Precipitation (mm)			
Year	Leaf	Scape	Leaf	Scape	1-Oct. to 1-Feb.	1-Feb. to date of max. scape length	1-Oct. to date of max. scape length	Scape growth rate (cm/wk)
1999	23.1 ± 1.0^{ab}	22.6 ± 2.5^{na}	3-Apr	20-Apr	220	174	394	na
2000	23.6 ± 1.2^{abc}	22.8 ± 0.9^{a}	27-Mar	10-Apr	181	266	447	6.0^{a}
2002	28.0 ± 1.5^{cd}	31.6 ± 1.3^{b}	12-Mar	18-Apr	348	30	378	10.4^{b}
2003	26.6 ± 0.7^{bcd}	24.9 ± 0.6^{a}	23-Mar	13-Apr	340	154	494	6.8^{c}
2004	22.1 ± 0.9^{a}	23.0 ± 1.3^{a}	24-Mar	7-Apr	290	102	392	5.5^{a}

in both cases). All of these corms combined from both sites at the end of the growing season in late April, showed an overall mean volume of 1.30 ± 0.061 cm^3 ($n = 120$).

Depths of these *Triteleia* corms in the soil were not significantly different in the paired longest and shortest plants dug in Vina and Barn populations (long-plant and short-plant corms combined at a site to compare Vina vs. Barn, $P = 0.112$; Vina and Barn corms combined to compare all long vs. all short corms, $P = 0.090$). Mean depth (±SE) for these combined corms (from soil surface to top of the corm) was 7.27 ± 0.29 cm ($n = 120$).

Corm volume correlated with scape length and number of flowers. The correlation coefficient for corm volume and scape length was 0.612, and for corm volume and numbers of flowers was 0.610 (both correlations significant at $P = 0.01$). In addition, at Vina and Barn in 1998, we found number of flowers per plant to be strongly correlated with scape length (Spearman's $r_s = 0.814$, $P = 0.001$, $n = 120$).

Corm volume and changes in mass through the spring. Only the 28 February volume was significantly different from each of the four volumes measured later ($P \leq 0.017$), and none of the March and April volumes differed significantly from each other (Fig. 5). There was close to a linear increase in volume through this 8-week study period, and the deviations of the sample means did not differ significantly ($P < 0.001$).

The preceding volume and depth data reported were obtained with the corm coat present on the outside. However, removing a *T. laxa* corm coat showed that the corm present at the beginning of the warm growing season (i.e., starting in February) had two parts. The first (referred to as the "old" corm), shrinks as leaves and scape lengthen on the growing plant; this older part was gradually replaced by an enlarging "new" corm on top of the old corm (not necessarily at the same rate in all plants of a population) (Fig. 4b). Dry mass for five dates measured starting in February 2002 (during the enlarging of the new corm, while leaves and scapes were growing), increased from about 210 to 547 mg (Fig. 5). Masses of the old corm, (not given in Fig. 5), were quite similar to each other, with means ranging from about 25 to 41 mg. An old corm is shown below the new corm in Fig. 4c.

New growth of corms in the wet season. In 2004, there was rain early in the wet season (67 mm from 17 to 26 October, when temperatures of air and soil were still warm, and 107 mm total by November 30). For corms dug at Vina on 1 December 2004, volume (mean ± SE) was 1.23 ± 0.08 cm^3. All these plants sampled in December

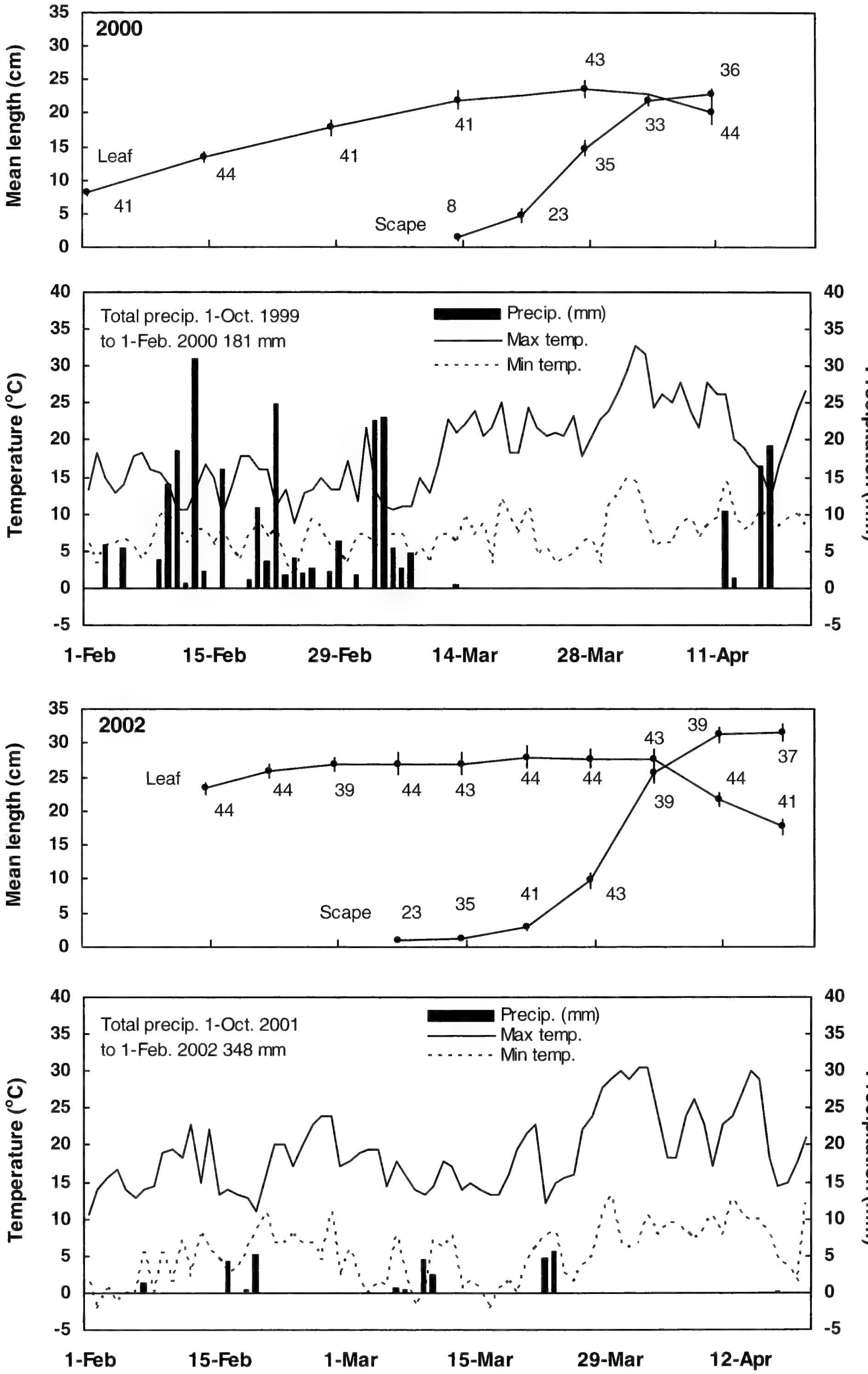

FIG. 2. Vegetative phenology for *Triteleia laxa* shown by mean (±SE) leaf and scape lengths at Vina during four years of the study. Daily precipitation and daily mean maximum and minimum temperatures at Orland, Glenn County (U.C. Davis 2005), are shown below each year's phenological data. Total wet season precipitation preceding 1 February is indicated in upper left corner for each year. N's are shown adjacent to the point of each sampling date.

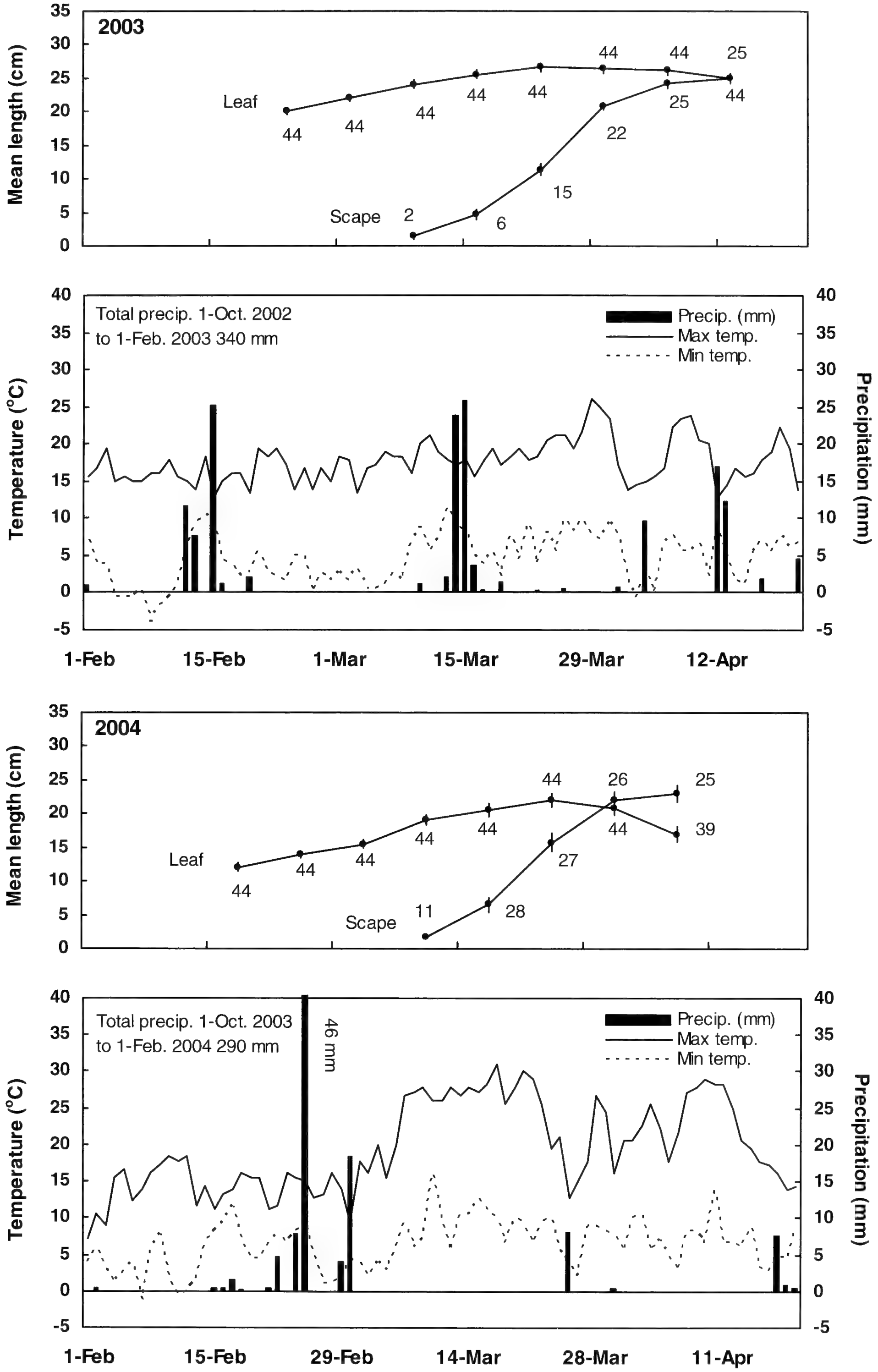

FIG. 2. Continued.

(n = 30) had a new, green shoot extending upward from the corm (mean length = 6.6 ± 0.45 cm), but no shoots had reached the soil surface. Mean (±SE) dry mass for the 30 plump and turgid new corms was 150 ± 3.8 mg, and for the shrunken old corm still attached (i.e., functional during early spring plant growth in 2004), 31 ± 3.3 mg. Seven of the 30 corms had

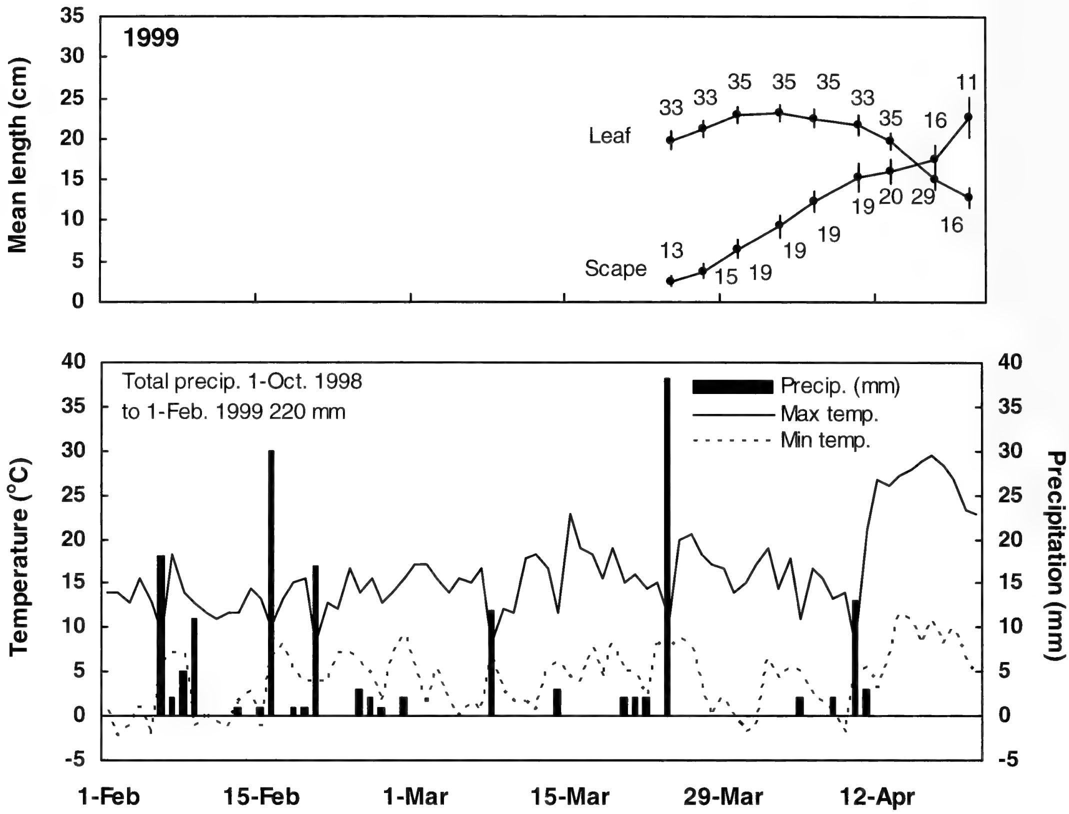

FIG. 3. Vegetative phenology for *Triteleia laxa* shown by mean (±SE) leaf and scape lengths at Vina in 1999 (a year scapes died before flowering). Daily precipitation and daily mean maximum and minimum temperatures at Orland, Glenn County (U.C. Davis 2005), are shown below the phenological data. Total wet season precipitation preceding 1 February is indicated in upper left corner. N values are shown adjacent to the point of each sampling date.

remains of the old corm from two years earlier (the corm functioning in 2003) still attached below the old corm.

None of the corms dug during any of the years of this study possessed additional small cormlets, derived vegetatively from the main corm, that have been reported elsewhere for *T. laxa* and have been used in horticultural propagation; however, geographical variation in cormlet production has been noted by (Hoover 1941).

Breeding System and Pollination

Compatibility. In 1998, a single flower was bagged on each of 37 plants; only 1 flower produced a fruit, whereas all plants produced fruits from unbagged flowers. In 2000, a few seeds were produced in both types of hand self-pollinations, within flower (autogamous) and within plant (geitonogamous) (Fig. 6). Seed numbers did not differ statistically in these two types of selfings ($P = 0.946$); the few seeds observed suggests a high degree of self-incompatibility in this population. As indicated in Fig. 6, hand cross-pollinations (xenogamous) and open-pollinated controls did not differ from each other in seed number ($P < 0.119$). Both produced highly significantly more seeds than the self-pollinations ($P < 0.0001$). In 2004, among the 36 covered plants, 23 made one or more fruits. However, 26 of the 40 fruits total sampled from these plants had no seeds, giving a mean (±SE) of 1.1 ± 0.3 seeds set per fruit; the 14 plants with fruits that contained one to six seeds had a mean of 3.0 ± 0.4 seeds per fruit. The 39 uncovered plants produced a mean of 16 (±1; range 1–40) seeds per fruit ($n = 78$), and all of these plants had at least two fruits with three or more seeds. Seeds per fruit were very significantly lower in covered (autogamous) than uncovered (open pollinated) flowers ($P < 0.0001$).

Stigmatic receptivity and changes in floral morphology. Flowers remain open for up to four or five days. Anthesis occurs from the period when flowers are about to open to about one to two days old (flower phase A to C). Stigmas become receptive following anthesis; thus flowers are protandrous. Anthers are located towards the center of the flower during anthesis, after which point the stamens reflex towards the perianth, separating the anthers from the stigma. The

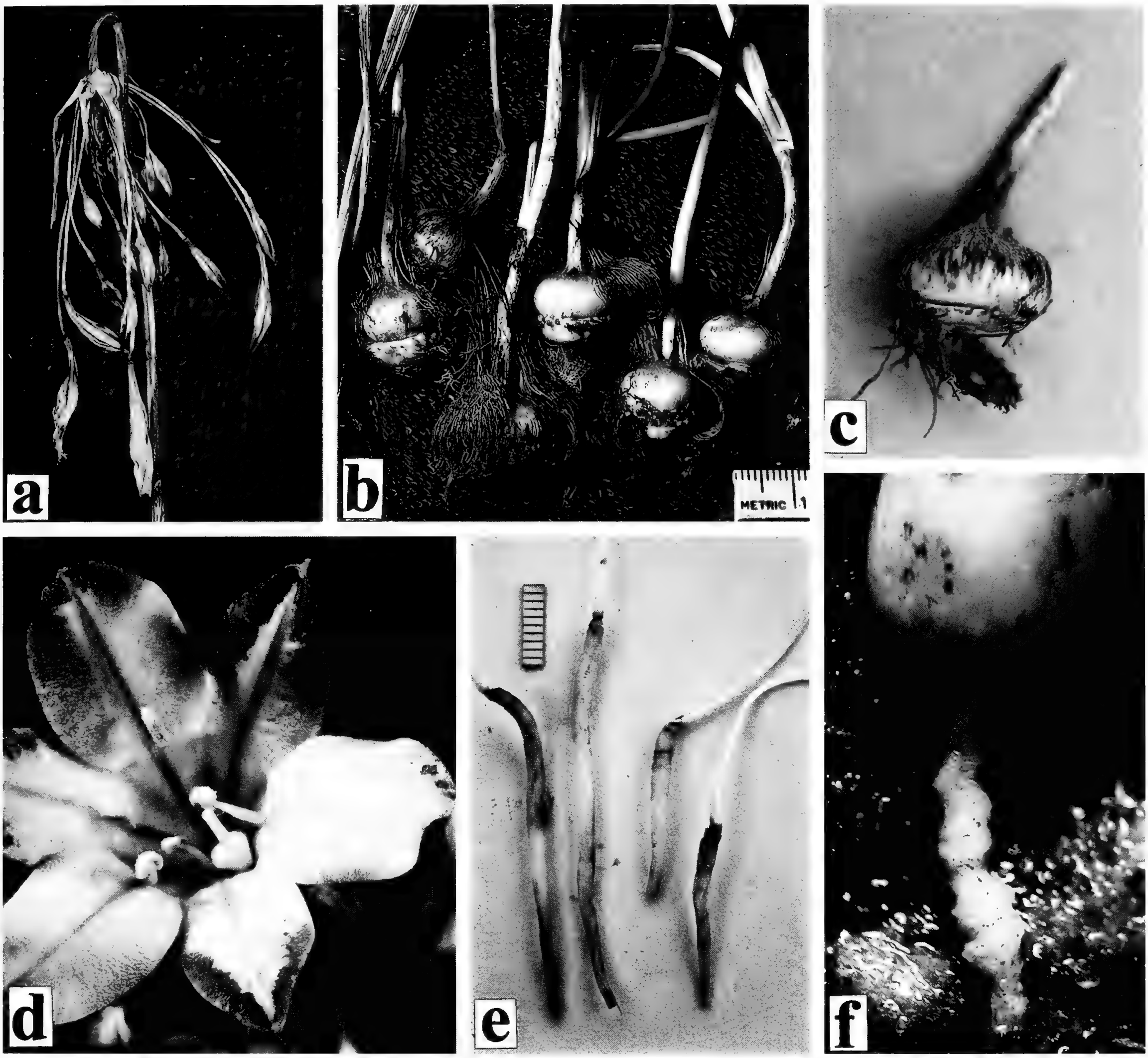

FIG. 4. Portions of *Triteleia laxa* plants. a. Dead scape, which bent and dried before flowers fully opened (scape from base to bend ± 150 mm). b. Corms in mid-spring, with new corm developing on top of the old while leaves and scape still green aboveground (smallest increments on ruler in mm). c. New corm at end of growing season, with dried remnant of old corm pulled down (corm ± 16 mm diam.). d. Flower with an older pistil lying against the perianth, with style bent towards center of the flower and stamens empty of pollen (corolla ± 18 mm diam.). e. First-season seedlings, showing thick contractile roots which have replaced the fine primary roots; note transverse lines on several roots indicating areas of initial contraction (scale = 10 mm). f. Young corm (±4 mm diameter) on seedling at end of first growing season, with shortened (corrugated) section of the contractile root below it.

gynoecium lengthens from flower phase A to D, coming to rest on the lower-most tepals, and curves inward towards the center of the flower as the flower droops towards the ground (Fig. 4d). As flowers age the stigma becomes noticeably more glandular, presumably to promote pollen reception. As flowers reach phase D they begin to turn brownish due to loss of some pigmentation, and presumably become less attractive to visitors. Results of the peroxidase assay (Fig. 7) show an approximate linear increase in peroxidase activity in the stigma as flowers age. Peroxidase activity (PA) increased significantly from phase A to phase C, and phase D had greater PA than all other phases ($P = 0.05$). At the earliest flower phase (A), 96% of stigmas showed no PA (no blue color), but by phase D, 40% of stigmas had the highest ranking.

Pollen-ovule ratios. Counts of pollen grains and ovules in one flower bud from each of 35 plants showed: (mean ± SE) 1) 20,500 ± 1760 pollen grains per anther, 2) no difference between upper-tier ($n = 18$) and lower-tier anthers ($n = 17$) ($P = 0.64$), and 3) 40.1 ± 1.0 ovules per ovary. The mean pollen-ovule ratio was 3090 ± 260 (range

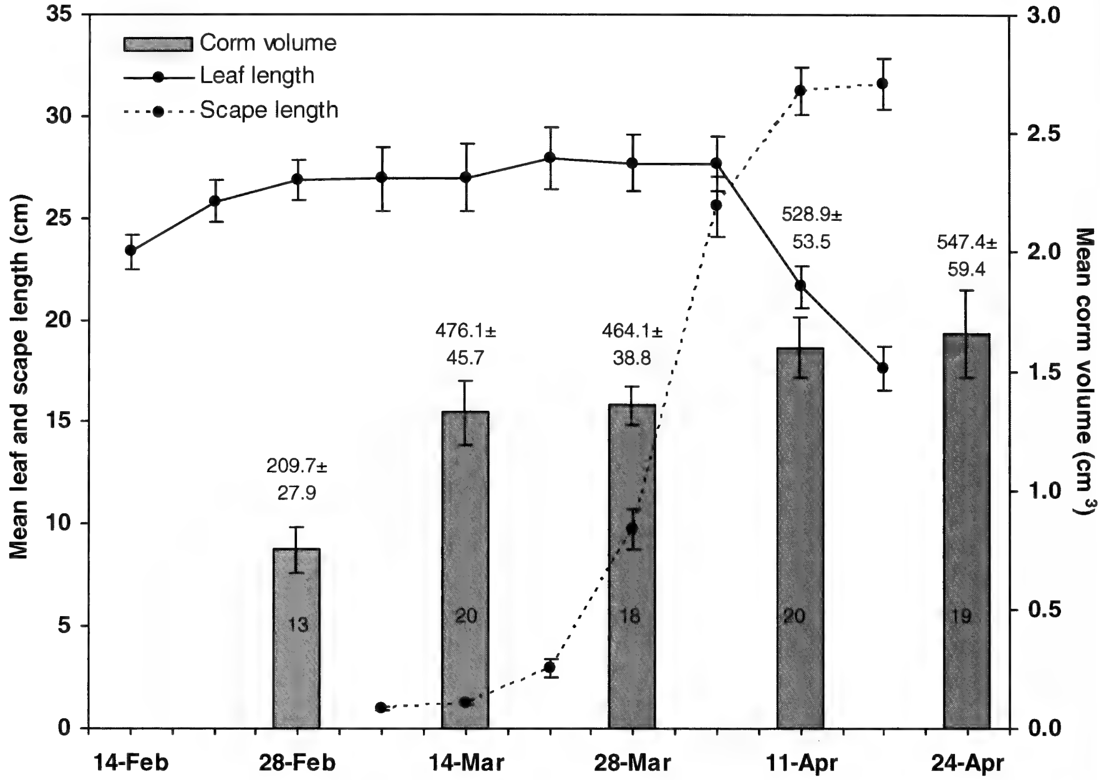

FIG. 5. Mean corm volume and mass in relation to mean leaf and scape length during the above-ground growing season in 2002 at Vina. Mean corm dry mass (mg) is given above each column. Sample size (n) for corm volume was 20 on every date; n's for corm dry mass are given inside columns; n's for leaf and scape length are given in Fig. 2. All error bars represent one standard error.

575–7250 grains per ovule); this result is consistent with the determination that flowers are outcrossing (Cruden 1977).

Nectar. A number of flowers tested had readings at the top of the refractometer scale (50% sucrose equivalents (SUE)), suggesting even higher SUE in these nectar samples. Mean ± SE of SUE was 44.1 ± 2.0%. Since readings were taken in the afternoon (4–6 pm DST), it is possible (but unlikely, due to the depth of corollas in bagged flowers) that there had been some evaporation of water from nectar, potentially biasing readings upward.

Reproductive Output: Flowers, Fruits and Seeds

Variation in numbers of flowers and fruits by year and by site. Significant differences in numbers of flowers were produced on the marked plants at the main study site at Vina during the five years they were available. Mean flowers per plant (±SE) in 2002 (12.6 ± 0.6; n = 50) was very significantly higher than all other years except 1998 (11.5 ± 0.9; n = 46) ($P < 0.0001$; Fig. 8). Fewer complete data sets on flowers per plant were available from our other sites, but we were able to complete an ANOVA comparing different sites through several years (Vina 2002–2004 with Park 2003–2004 and Road 2003–2004). As noted in Table 2, Tukey HSD comparisons indicate many significant differences between these three sites in 2003 and in 2004 (and also between the two years for Park and Road sites).

Data on fruits per plant showed significant differences among the five years at Vina and also among sites in 2002, 2003, and 2004 (Fig. 8 and Table 2). Table 2 also shows comparisons of % fruit set (the proportion of flowers producing fruits). Additional determinations of % fruit set (mean ± SE, range, n) from Vina and Barn were not included in the ANOVAs: Vina in 1998 (75.7 ± 2.3, 40–100, 46) and in 2000 (69.1 ± 3.5, 16.7–100, 34); Barn in 1998 (60.0 ± 5.0, 0–100, 34) and in 2000 (68.8 ± 5.7, 0–100, 29).

Variation in numbers of ovules per ovary, seeds per fruit, and percent seed set. Ovules that did not develop into mature seeds were still present in mature fruits and distinguishable under a dissecting microscope. The vast majority of undeveloped ovules recorded appeared to have not developed at all, although there were also a number that reached nearly full seed size but

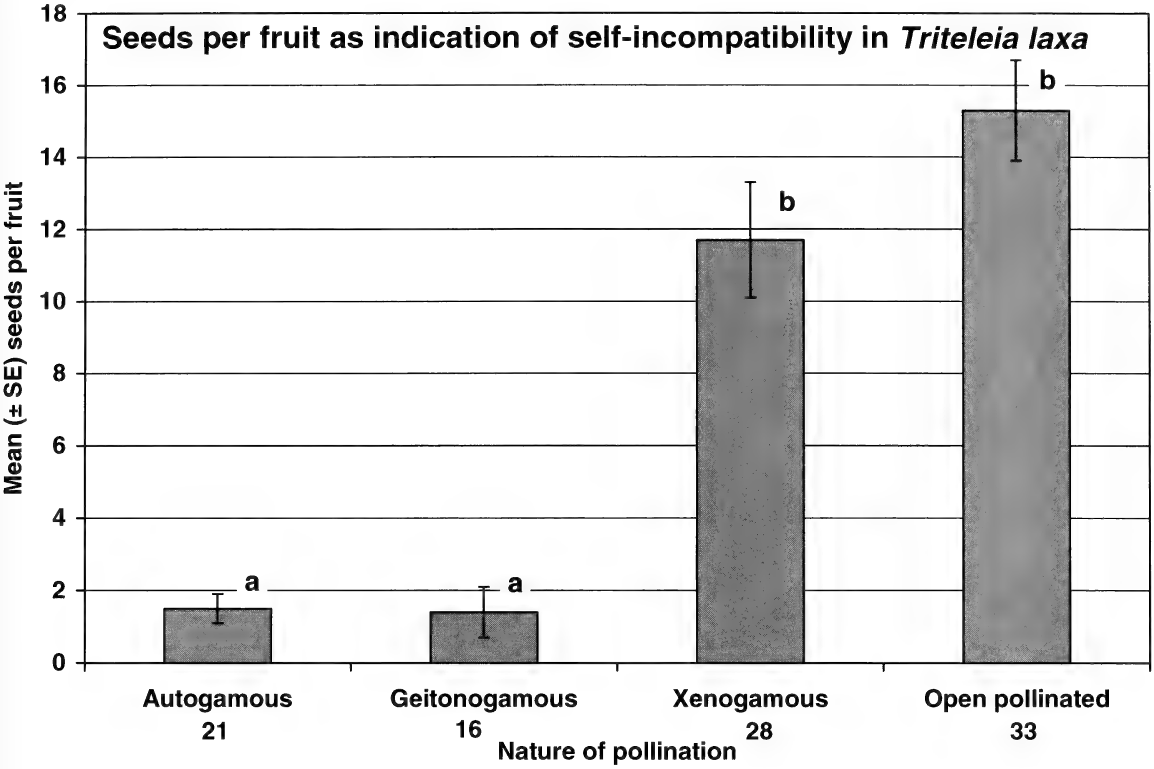

FIG. 6. Seeds per fruit (mean ± SE) in *Triteleia laxa*, resulting from three types of hand pollinations, compared with open-pollinated (control) plants at Vina in 2000. Sample sizes are shown below the x-axis labels. ANOVA and Tukey HSD comparisons were performed, and seed means with the same superscript letters at tops of columns do not differ significantly.

were pale and shrunken or caved-in. Counts from the largest samples of ovules and seeds are shown for three years at Vina (Table 3) and also in a comparison of three sites for 2003 (Table 4). Additional counts of seeds per fruit in earlier years at Vina and Barn (not included in these tables or the ANOVAs) are close to the 2004 count for Vina shown in Table 3. These earlier counts of seeds per fruit include (mean ± SE, range, n) Vina 1998 (14.8 ± 0.8, 1–33, 72); Vina 2000 (14.9 ± 1.1, 5–31, 33); and Barn 2000 (13.9 ± 0.9, 3–25, 39). Scapes that escaped the disease in 1999 were subjectively sought out, and showed lower numbers of seeds per fruit: Vina (11.3 ± 1.4, 2–26, 23), and Barn (11.0 ± 0.1, 0–24, 44).

Seed Mass, Viability, and Germination

Collected seeds showed no difference in mg per seed (mean ± SE): 1.660 ± 0.047 in garage and 1.753 ± 0.066 in lab (n = 40 each site; t = 1.154, P = 0.25). From all sites, collected seeds had 100% viability (n = 50 seeds each site).

Seed germination.. Before the planting on 30 November 2003, 115 mm rainfall had already occurred in south Chico (U.C. Davis 2005). Fortuitously, 28 mm occurred in the first two days after planting, and 191 mm total rainfall between planting and the first excavation of seeds on 28 December. There had been a total of 615 mm precipitation by the time these seedlings were drying up and the study was concluded (9 April 2004). Regional precipitation during this period was not obviously different from the preceding years (Fig. 1).

Table 5 shows that many seeds germinated in only four weeks. It was difficult to find the tiny seedlings among soil aggregates, and in four weeks after planting only 20 of the first 50 seeds were found as seedlings, along with 19 additional ungerminated seeds. Sizes of the seedlings in batches at 6 wk and later suggest that germination was well underway in four or five weeks after first wetting. Later batches of seeds showed germination percentages of 82–98%.

Seedling Growth. The sprout (cotyledon and rest of the seedling) continued to elongate, and in 8 wk the first foliage leaf of the seedling emerged from the somewhat sheath-like and still-elongating cotyledon. Leaf length of a seedling was measured from where it departed the cotyledon, to its tip. In 10 wk, leaves appeared green, some nearly above the soil surface; in 12 wk, most leaves extended above the soil surface, and by 18+

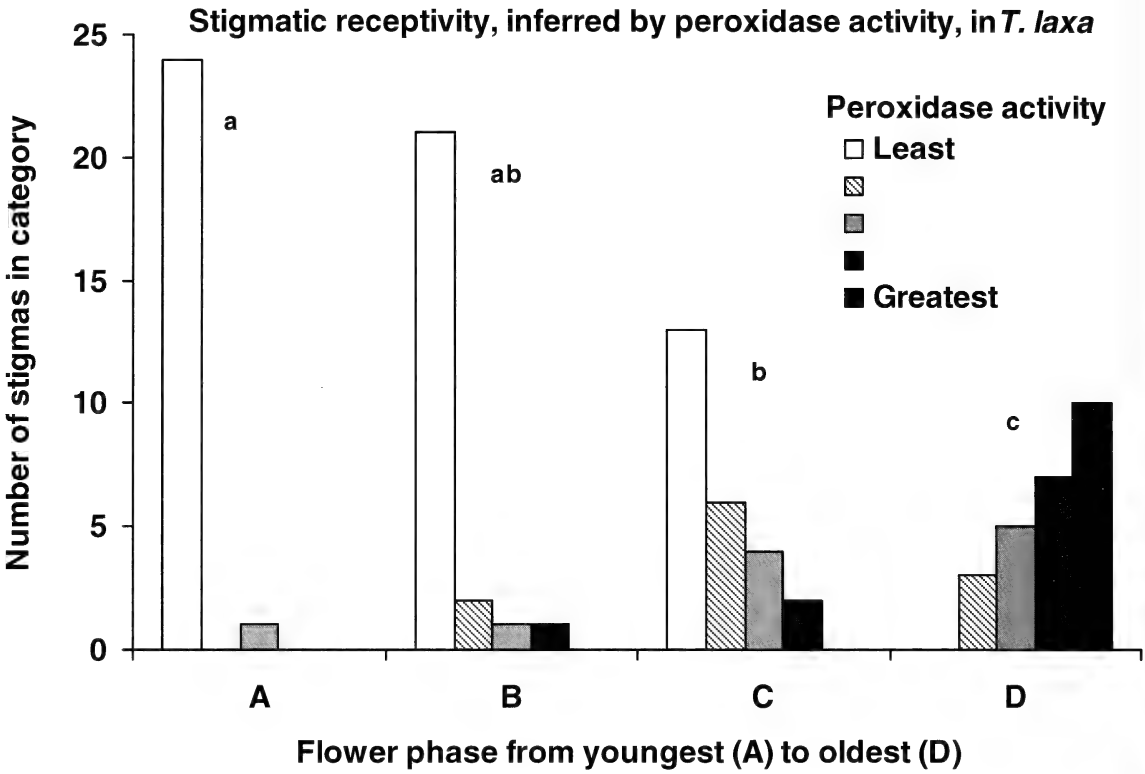

FIG. 7. Results of colorimetric assay in *Triteleia laxa* stigmas, showing increase in stigmatic peroxidase activity in relation to flower phase. Flower phases: (A) flower buds nearly open; (B) flowers recently opened and anthers dehisced (1–3 d old); (C) flowers with anthers empty, and with the style bent towards the middle of the flower (2–4 d old; Fig. 4d); and (D) flowers recently closed and most without any sign of seed formation yet (4–6 d old). Stigma coloration was ranked on a 0–4 (least to most) scale, based on the amount of stigmatic area covered and intensity of the color (n = 25 for each flower phase). ANOVA and Tukey HSD comparisons were performed; flower phases with the same superscript letter above their columns do not differ significantly (alpha = 0.05).

weeks (9 April) most leaves were yellowing and dying—representing the end of their winter/spring growth.

As the sprout continued to lengthen downward a thick lateral root emerged. A "pinching in" was discernible on the sprout by week 14, from which it was possible now to separately measure root (extending distally from this point), and shoot (the rest of the sprout extending back to the seed).

Two noteworthy features were observed from week 14 through week 18. At the base of the shoot by week 14, a slight swelling occurred, which later developed into the seedling's corm, the only part of the seedling to remain alive during the up-coming summer drought (Fig. 4e). Diameter of the corm (mean ± SE, at its widest, to the nearest 0.5 mm) increased from 2.4 ± 0.1 (n = 43) on week 16 to 3.2 ± 0.1 (n = 41) on week 18. On these weeks the thick lateral root, along the 2 or 3 cm immediately below the developing corm, appeared corrugated or twisted and thickened (Fig. 4f), and appeared to have a loose, transparent sheath around it in this region. Internal anatomy was not investigated, but this region certainly represents the "shortening" part of a contractile root, shown for other monocotyledonous geophytes, where growth changes in root cortex cells permit collapse of layers in cortex tissues, and cause the epidermis to loosen and become sheath-like (see Rimbach 1902; Smith 1930; Jernstedt 1984; Putz 1996). Table 5 shows that this root (below the corm) was indeed shorter in week 16 than in week 14. The degree that the contractile root helped move the seedling deeper into the soil was not investigated.

DISCUSSION

Phenology and Growth of Leaves, Scapes, and Corms

In the five years we observed vegetative phenology, we found that flowering plants each produced two leaves during the winter; leaves continued to elongate until mid March or early April. We did not find a correlation between yearly maximum leaf lengths and the amounts of precipitation. We have numerically documented that at maximum leaf length, the old corm, which

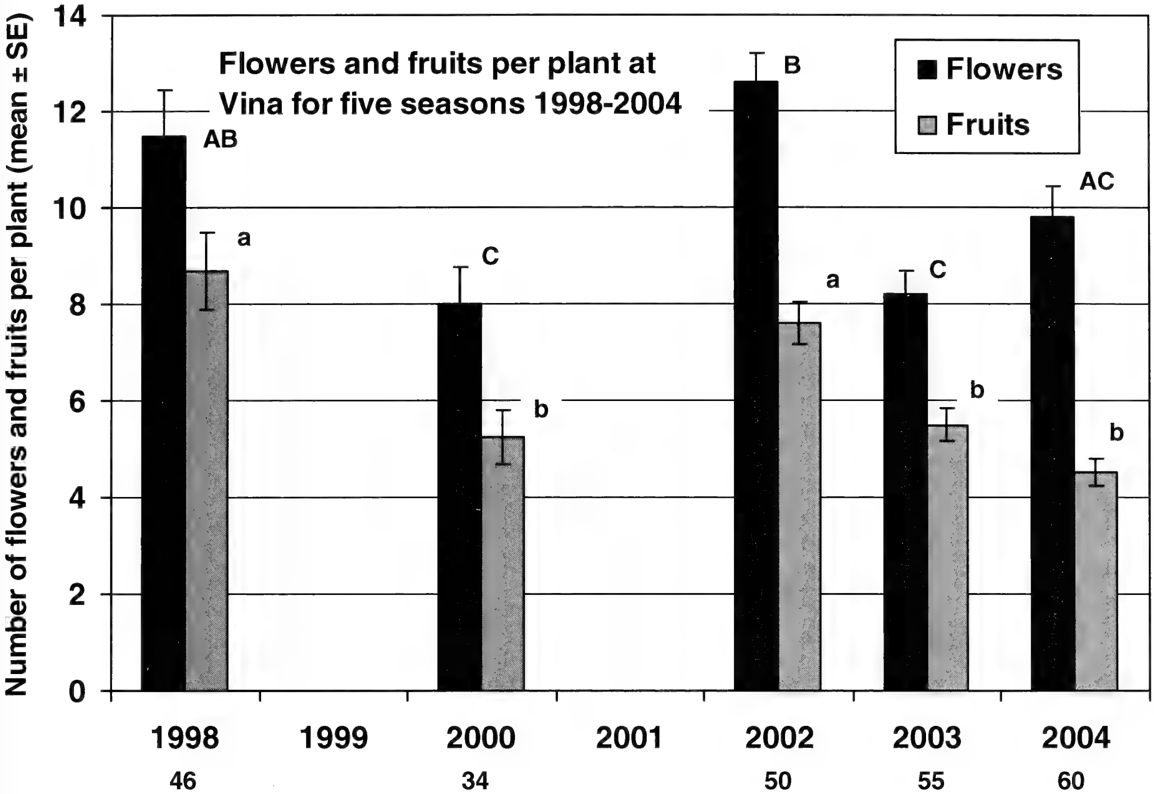

FIG. 8. Mean (±SE) numbers of flowers and fruits per plant in *Triteleia laxa* at Vina, for the five years of successful reproduction from 1998 through 2004. N, the number of plants, is shown below the year. ANOVA and Tukey HSD comparisons were performed; means with the same superscript letters (flowers per plant, upper case; fruits per plant, lower case) do not differ significantly. Blank areas are left for 1999 and 2001 to emphasize the essential lack of flower, fruit and seed production in these two of the seven years of this study, due to the scape disease described in the text.

was giving rise to the leaves, had already produced a new corm on top of itself—before the plant had even flowered. Niehaus (1971) has described similar timing of new corm growth for species of *Brodiaea*.

The old corm also produced the flowering scape (for the anatomical site of scape origin in the old corm, see diagram for *Triteleia hyacinthina* in Smith 1930). Scape growth and maximum length (=height), and also the start of flowering may be influenced by daylength, as well as by the photosynthates produced by the leaves and the green scape itself. Maximum length was reached in a relatively narrow time period (about two weeks). It is not clear how many environmental factors influence maximum scape length, but the negative correlation between total amount of spring rain and scape length suggests that in some years (e.g., 2002; Table 1) scapes may be taller with *less* rain, and that air and soil temperatures and/or timing of the rain all have important influences. However, Niehaus (1971) reported that length of scape in species of *Brodiaea* varied according to the amount of moisture during the growing season, with the scape 50% shorter in drier years (no measurements were given).

We have not studied summer dormancy in *T. laxa* corms, but have excavated corms at different times of the year. Rees (1989) described a "physiological advantage" existing in geophytes, in that corms that appear "dormant" may be producing primordia and early tissue growth well before environmental conditions promote expansive growth. Niehaus (1971) stated that corms in California species of *Brodiaea* show some underground growth, with both shoot and root emergence, even prior to the first winter rains. Keator (1967) reported that species of *Dichelostemma* vary in initiating root growth, most species only after several rains, and with only the early-flowering *D. capitatum* Alph. Wood showing any shoot growth after the first rains. We have provided quantitative information on early growth in *T. laxa*, on corm mass and volume, and on length of shoots after several rains, but still early in the wet season (e.g., by 1 December 2004, green shoots from 30 corms averaged 6.55 cm long, all still below the soil surface). More study on this topic could be

TABLE 2. YEAR AND SITE COMPARISONS OF MEAN ± SE (AND RANGE) FOR FLOWERS PER PLANT, FRUITS PER PLANT AND % FRUIT SET IN *TRITELEIA LAXA* AT THREE SITES IN 2002–2004. ANOVA and Tukey HSD comparisons were performed separately for each parameter listed. In each column, means with the same superscript letters do not differ significantly. For flowers, $P < 0.001$ for all significant differences except Park vs. Road in 2003 with $P < 0.05$; for fruits, all significant differences at $P < 0.001$ except Park vs. Road in 2003 with $P < 0.005$, and Vina 2002 vs. Vina 2003 with $P < 0.05$; for percent fruit set, all significant differences with $P < 0.001$ except Vina 2002 vs. Vina 2003 with $P < 0.05$.

Year and site	n	Flowers per plant	Fruits per plant	% fruit set
2002				
Vina	50	12.6 ± 0.6^{acd} (5–25)	7.6 ± 0.4^{de} (3–14)	60.7 ± 2.0^{bcd} (33.3–87.5)
2003				
Vina	55	8.2 ± 0.5^{ab} (2–19)	5.5 ± 0.3^{abc} (2–16)	69.6 ± 2.7^{de} (33.3–100)
Park	51	12.6 ± 0.8^{cde} (3–29)	8.6 ± 0.6^{def} (3–22)	70.1 ± 2.3^{def} (33.3–100)
Road	53	15.7 ± 1.1^{df} (3–37)	11.5 ± 0.8^{ef} (2–27)	74.4 ± 2.1^{def} (43.5–100)
2004				
Vina	60	9.8 ± 0.7^{abc} (4–28)	4.5 ± 0.3^{ab} (1–12)	49.8 ± 2.6^{a} (16.7–100)
Park	52	7.9 ± 0.4^{a} (4–14)	3.9 ± 0.3^{a} (0–10)	52.2 ± 2.8^{ab} (0–85.7)
Road	52	14.1 ± 0.8^{def} (3–30)	7.4 ± 0.5^{cd} (1–19)	54.7 ± 2.4^{abc} (7.8–85.7)

interesting, especially in determining if late dry season/early wet season growth also occurs in *T. laxa* or other geophytes occurring at considerably higher (colder) elevations in mediterranean California.

Corm depth did not differ significantly when large numbers of shorter and longer flowering scapes were compared; this may be the "standard" depth to which the corms are delivered by several seasons of contractile root activity (see below) in the clay loam soils here.

Although depths did not differ, the corm *volumes* were highly significantly different, with the longest scapes attached to the largest corms. Surprisingly, Han (2001) reported that heights of scapes were not related to corm sizes for (mainly garden-grown) *T. laxa* and several other California geophytes (*T. bridgesii* (S. Watson) E. Greene, *T. ixiodes* (S. Watson) E. Greene, and *Dichelostemma ida-maia* (Alph. Wood) E.Greene). However, number of flowers per scape in *T. laxa* was found to be positively related to corm size by us and also by Han (2001). According to Han and Halevy (1993) these new corms can gain up to about 90% of their final weight even before flowering. Han (2001), who was growing live corms, indicated that *T. laxa* corms with a fresh weight of 1.1 g or more do flower in greenhouse studies, but that typically commercial-sized corms weigh 2.5 g or more—a mass reached in three or four growing seasons. We expect that it also takes that long in the field to reach good flowering size, and expect that larger *T. laxa* plants seen in the field generally are older and have heavier corms. But in the related geophytic genus, *Dichelostemma*, Keator (1967) has noted that large corms do not guarantee flowering, and that environmental features of the current growing season (as well as stored reserves) may affect formation of flowers.

We have documented a feature of phenology and growth that seems to be un-recorded in literature about geophytes in the field. In two of the seven years of this study (1999 and 2001), most *T. laxa* plants at Vina and Barn produced apparently normal leaves, but failed to flower due to a disease causing death of the elongating scapes. We have recorded external symptoms caused by this pathogen (Fig. 4a; unpublished information), but have not determined the cause or found matching symptoms in the literature on wild plants. Superficial similarities in the disease referred to as "neck rot" (due to the fungus *Botrys allii*) can occur in the cultivated onion *Allium cepa*, where infection just below the umbel can result in "blasting of flowers" (Voss 1979). Also, Han and Halevy (1993) noted that *T. laxa* grown in Holland for commercial distribution

TABLE 3. YEARLY COMPARISONS OF MEAN ± SE (AND RANGE) FOR TOTAL OVULES PER OVARY, SEEDS PER FRUIT AND % SEED SET IN *TRITELEIA LAXA* AT VINA IN 2002, 2003, AND 2004. Total ovules includes undeveloped ovules as well as those maturing into seeds. ANOVA and Tukey HSD comparisons were performed separately for each parameter. In each column, means with the same superscript letter do not differ significantly ($P < 0.001$ for seeds, and $P < 0.0001$ for seed set).

Year, at Vina	n	Total ovules per ovary	Seeds per fruit	% seed set
2002	100	33.3 ± 0.6^{a} (15–46)	19.0 ± 0.8^{a} (3–39)	56.3 ± 1.8^{a} (10–91.7)
2003	98	31.5 ± 0.6^{a} (20–47)	18.4 ± 0.8^{a} (1–40)	57.7 ± 2.0^{a} (3–90.9)
2004	120	32.2 ± 0.5^{a} (14–49)	13.1 ± 0.7^{b} (0–36)	40.1 ± 1.9^{b} (0–94.7)

TABLE 4. SITE COMPARISONS OF MEAN ± SE (AND RANGE) FOR TOTAL OVULES PER OVARY, SEEDS PER FRUIT AND % SEED SET IN *TRITELEIA LAXA* IN 2003. ANOVA and Tukey HSD comparisons were performed separately for each parameter. Total ovules includes undeveloped ovules as well as those maturing into seeds. In each column means with the same superscript letter do not differ significantly ($P < 0.009$ for ovules, $P < 0.001$ for seeds, and $P < 0.032$ for seed set).

Site, in 2003	n	Total ovules per ovary	Seeds per fruit	% seed set
Vina	98	31.5 ± 0.6^{a} (20–47)	18.4 ± 0.8^{a} (1–40)	57.7 ± 2.0^{a} (3–90.1)
Park	102	34.0 ± 0.6^{b} (18–50)	13.5 ± 0.7^{b} (2–31)	$39.1 \pm 2/0^{b}$ (6–92.6)
Road	106	34.4 ± 0.5^{b} (21–47)	17.5 ± 0.8^{a} (4–43)	50.3 ± 2.2^{c} (10.8–97.1)

can be infected by three pathogens (*Corynebacterium fascians*, *Rhizoctonia tuliparum*, and *Sclerotinia bulborum*), but no symptoms were listed. Our discovery emphasizes the value of observing the same populations in the field for a series of consecutive years, to note possible stochastic events in the life cycle, as when sexual reproduction is prevented.

Features of Sexual Reproduction

As with many plants in mediterranean areas, the flowers, fruits, and seeds are produced as vegetative growth is completed near the start of the hot and dry summer season. By the time *Triteleia laxa* produces a scape with flowers in late March or April, air temperatures are higher, and flying insects are available for vectoring pollen among flowers. Our tests suggest that *T. laxa* is self-incompatible (Fig. 6), or has a degree of self-compatibility but relies on insects to vector pollen and promote out-crossing. According to comments by Cruden (1977) features that we observe in *T. laxa* are often associated with self-incompatible and out-crossing flowers, such as a large, showy floral display well up and above associated plants, a relatively high pollen:ovule ratio, and the presence of nectar. Berg (2003) has shown that nectaries in *T. laxa* are in the three septae that separate locules of the ovary, and that nectar is secreted into three nectar channels on the "shoulders" of the ovary. It would be interesting to determine if the tongues of any insects we observed visiting flowers, are able to extract nectar from these channels rather than strictly sucking it up from the pool that collects around the stipe at the base of the ovary. Outcrossing may be facilitated by these insect flower-visitors, and also by the protandry seen in these hermaphroditic flowers (Fig. 7).

Male and female functions in hermaphroditic flowers can be selected for by different mechanisms, and it is often found that factors that select for increases in male function in turn decrease female function, and vice versa (e.g., Charlesworth and Charlesworth 1987; Burd 1994). Protandry, the temporal separation of sexual functions in plants wherein the male function precedes the female function, may have evolved for reasons other than promoting self-incompatibility, such as increasing male function. In contrast, self-incompatibility decreases male function (due to need for self pollen to travel elsewhere) while increasing female function (avoidance of potentially fitness depressing self pollen). Lloyd and Yates (1982) suggested that one advantage to separation of sexual functions in hermaphroditic flowers may be increased opportunity for floral features to evolve via sexual selection. The protandrous flowers of *T. laxa* suggest the opportunity for female choice and male-male competition. Furthermore, stigmatic receptivity schedules can affect the density and diversity of pollen, and increased pollen tube density and pollen donor diversity can encourage sexual selection via male-male competition and female choice (Galen et al. 1986). However, we have not examined pollen density and diversity in this species; the opportunity for sexual selection may be minimized if sexual reproduction is pollen-limited (Willson 1979; Galen et al. 1986). Lastly, stigmatic receptivity schedules can play a strong role in reproductive output due to affecting density and diversity of pollen received (Galen et al. 1986) as well as rate of pollen germination and pollen tube growth (Yi et al. 2006).

Relatively low reproductive output has been found in both fruit set and seed set for *T. laxa* in our region (well documented with large sample sizes, in several sites, and over several years). There are generally two main factors likely to cause low fruit set and seed set: pollen (including pollinator) limitation, and abiotic resource limitation (Stephenson 1981). Slightly more seeds per fruit were found in our open-pollinated flowers than in our hand cross-pollinated flowers, suggesting that pollen limitation is not occurring. Although we have no direct measurements on abiotic features like local temperature and precipitation, the study period in spring of 2003 had high amounts of rain regionally, which we expect would rule out moisture as a limiting resource in that year. The highest proportion of fruit set was indeed in 2003, but that was still only between 69.6 and 74.4% at the three sites measured. Our data from 2004 are in agreement: fruit set at these same three sites (this time with unusually low spring rainfall in 2004) were lower, and may

TABLE 5. SEED GERMINATION AND GROSS MORPHOLOGY OF SEEDLINGS IN *TRITELEIA LAXA*, BASED ON SEEDS COLLECTED AT VINA ON 22 MAY 2003 AND PLANTED OUTDOORS IN GARDEN SOIL IN CHICO ON 30 NOVEMBER 2003. Length of "sprout to primary root tip" refers to the entire seedling length from seed coat to tip of the primary root before additional organs were discernible; at week 14 the primary root was shriveled and no longer measured. Length of "lateral contractile root" refers to the thick, new (lateral) root from its point of emergence near the seed to its tip; this contractile root had not yet "replaced" the primary root. Length of "contractile root below new corm" refers to the contractile root (which has replaced the primary root) from its base at the developing corm, to its tip (see Fig. 4e,f). Length "sprout to base of new corm" refers to length of seedling, from the seed coat to the base of the new corm. Length "leaf" refers to the leaf from its point of emergence from the sprout to its tip. Diameter of corm was measured at its widest point. Diameters and lengths (mean ± SE) are in mm. [a] Germinating seeds were difficult to discern among the soil aggregates and pebbles. N is probably low here because ungerminated seeds were simply not detected. Numbers recovered (of 50) in later batches are as high as 42 (82%) to 49 (98%). [b] Since only 20 seedlings were recovered, but additional seedlings from outside the 50-seed batch were available for this one date, an additional 23 seeds with sprouts were measured. [c] N is lower because specimens broken during excavation could usually not be measured with accuracy. [d] Seedlings were too breakable to extract intact from soil, and leaves were yellowing and drying; only corms were able to be measured well.

Date seeds excavated (weeks since planting)	Number seedlings recovered (50 seeds)	Length sprout to primary root tip	Length lateral contractile root	Length contractile root below new corm	Length sprout to base of new corm	Length leaf	Diameter corm
28 Dec 2003 (4 wk)	20[a]	1.5 ± 0.1 (n = 43[b])	—	—	—	—	—
11 Jan 2004 (6 wk)	37	3.8 ± 0.3 (n = 37)	—	—	—	—	—
25 Jan (8 wk)	42	7.9 ± 0.6 (n = 42)	—	—	—	2.3 ± 0.3 (n = 30[c])	—
8 Feb (10 wk)	49	19.6 ± 0.8 (n = 45[c])	—	—	—	15.5 ± 0.6 (n = 48)	—
22 Feb (12 wk)	46	23.9 ± 1.0 (n = 42[c])	8.4 ± 1.0 (n = 29)	—	—	29.4 ± 1.2 (n = 38[c])	—
7 Mar (14 wk)	46	44.1 ± 1.7 (n = 44[c])	—	29.8 ± 1.2 (n = 44[c])	14.4 ± 0.8 (n = 44[c])	50.7 ± 1.3 (n = 45[c])	—
21 Mar (16 wk)	43	—	—	20.1 ± 1.5 (n = 32[c])	20.1 ± 1.5 (n = 32[c])	64.6 ± 1.4 (n = 43)	2.4 ± 0.1 (n = 43)
9 Apr (18+ weeks)	41[d]	—	—	—	—	—	3.2 ± 0.1 (n = 41)

reflect plant reproduction suffering from drought of an "early mediterranean summer."

A possible cause for the relatively low proportion of ovules developing into seeds (Tables 3 and 4) could be a polyploid condition in the populations studied. Davidson (1975), using *Triteleia laxa* plants previously collected from different localities, but then growing at the Rancho Santa Ana Botanical Garden, documented diploid, tetraploid, and hexaploid conditions in this species. Source localities were not given, but he found percent of "good pollen" (as opposed to empty grains) varied somewhat in populations according to ploidy level. Although most diploid ($2n = 16$) as well as most polyploid ($2n = 28$, 32, or 48) plants produced 85 to 98% good pollen, one population with $2n = 28$ and one with $2n = 48$ produced only about 60% good pollen, associated with "lagging" meiotic chromosomes. In addition to affecting microspore formation, such meiotic irregularities could also cause some ovules to be inviable, and could account for the many tiny, white ovules, that did not seem to have grown at all, found among ripe seeds in mature fruits in our study.

Features of the Seed and Seedling Stages in the Life Cycle

We found that 100% of the plump and black *T. laxa* seeds were viable, and that 80–90% of these seeds germinated (Table 5). While Emery (1988) noted that no specific conditions are needed to get germination in this species, Han (1993) noted that eight weeks of cold stratification is needed to get high percentages of the seeds to germinate. We found that four weeks of ambient temperatures outdoors in December produced high percentages, possibly due to our storage methods having subjected seeds to alternating temperatures during both summer and fall.

Most of the early seedling growth occurs underground during the winter; several of the features we have found for *T. laxa* have been briefly described for other geophytes a century ago by Rimbach (1902). The seedling of *T. laxa* has a contractile root, a structure now listed as widespread in geophytic monocots (Putz 1992, 1996) and that probably functions best in winter, when the soil is wet and is most penetrable. We suspect that the "channel effect" described for contractile roots of seedlings and also for older stages of geophytes including *T. hyacinthina* (Putz 1992, 1996) pertains to *T. laxa*. That is, the space or channel provided by the contractile root first growing wide and thick will later permit passageway (a channel) for the sinking of the developing corm as this root shrinks and pulls the rest of the growing seedling deeper into the soil. The increased depth of a seedling's corm (or bulb) achieved during the wet months by a contractile

root, presumably promotes survival during the intensely hot and dry conditions occurring nearer the soil surface during the mediterranean summer. Possession of deep-seated corms is usually considered an advantage of the geophytic habit (e.g., Rees 1989). Putz (1996) noted that second-year (or even older) plants of many geophytes (including *Brodiaea*, according to Niehaus 1971) can produce new contractile roots that help seat the corms even deeper.

Seedlings of some California geophytes have been described earlier with relatively little detail (e.g., Rimbach 1902; Keator 1967; Niehaus 1971), or occasionally with considerable anatomical detail (Jernstedt 1984). We have documented the size and behavior of *T. laxa* seedlings more quantitatively (Table 5), and show that a single green leaf extends aboveground 5 or 6 cm, and that a tiny corm forms, averaging 3.2 mm wide, before the seedling goes into a dormant state with the approach of mediterranean summer. This production of a small over-summering corm during the wet season is certainly a signature of survival in a geophyte seedling.

We have documented many aspects of the field biology for *T. laxa*, but gaps in our knowledge remain. We do not know how long it takes in the field for a seedling to produce a plant that flowers, or for how many years a plant flowers or persists. It also would be interesting to investigate the extent to which corms and aboveground organs are consumed by animals. We believe our data do provide ample background information to stimulate field studies on other species of *Triteleia* and other mediterranean geophytes.

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GIANT SEQUOIA (*SEQUOIADENDRON GIGANTEUM* [TAXODIACEAE]) SEEDLING SURVIVAL AND GROWTH IN THE FIRST FOUR DECADES FOLLOWING MANAGED FIRES

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ABSTRACT

Giant sequoia (*Sequoiadendron giganteum*) seedling survival was nearly seven (6.78) times greater in heavily charred soils than in non-burned soils 34 and 35 yr after the first experimental burns in Kings Canyon National Park, California, and the first such management burns in any western national park. Tree height, especially trees growing in intensely burned areas, was found to be highly correlated with sunlight and less so with moisture. Moisture and light were important to establishment of giant sequoias but continued growth of these trees in the first four decades of life appears to be more dependent on high levels of sunlight. Surveyed vegetation and downed wood indicated that 35 yr after management burns stand structure has developed to the point where the management areas are susceptible to destructive crown fires.

Key Words: Giant sequoias, *Sequoiadendron giganteum*, seedlings, survivorship, fire.

Fire is necessary for giant sequoia (*Sequiadendron giganteum* [Lindl] Buchh.) reproduction. It removes surface litter and duff and opens up the forest canopy (Kilgore and Biswell 1971) thereby creating the conditions necessary for seedling germination and growth of what (Stephenson 1994) described as a "pioneer species" (one that requires a "canopy-destroying disturbance to complete its life cycle"). Conversely, it is known that few to no giant sequoia seedlings become established in the thick duff of infrequently burned groves (Kilgore and Biswell 1971; Hartesveldt and Harvey 1967; Hartesveldt et al. 1975; Harvey et al. 1980). While the intensity and duration of fire necessary to promote effective reproduction is still a matter of controversy (Stephenson et al. 1991; Stephenson 1996), it is known that hot fires burning in dense stands of mature giant sequoias produce as many as 100,000 seedlings per hectare following heat-induced seed fall (Hartesveldt et al. 1975). Hot fires, however, also threaten groves if they have a "fire-ladder" type of vegetation that allows fire to spread into the canopy (Parsons and Botti 1996; Stephenson 1994).

The present study reports on the growth of young giant sequoias and factors affecting their survival following experimental fires set in 1965 and 1966 in Redwood Canyon, Kings Canyon National Park. At the time they were set, these fires were the first experimental burns in a coniferous forest ecosystem in a western national park. The associated Hartesveldt Study (Hartesveldt et al. 1975; Harvey et al. 1980) and subsequent research (Harvey and Shellhammer 1991) is a rare long-term study in which over 7000 seedlings established after the original management fires were individually identified and have been monitored since. The objective of the present work was to identify key factors affecting their growth during the 35 yr following the controlled burns. We also report on the build up of duff, litter, downed wood, and of the subcanopy of trees and bushes between the time of the burns in 1965 and 1966 and this study in 2000.

METHODS

Four study areas were established as controlled burn sites in the Redwood Mountain Grove of Kings Canyon National Park, California, in 1964–66. Giant sequoia seedlings did not survive past five years post-burn in two of the areas, Ridge and North, due primarily to shading by dense tree cover in Ridge Area or dense ground cover (primarily *Lupinus* spp.) in North Area (Harvey et al. 1980) but individuals persisted to 2000 in the other two areas, i.e., Trail, burned in 1965, and South, burned in 1966 (Figs. 1 and 2). The manipulated portions of these two areas are approximately 1.8 hectares each and both have a base elevation of 1611 m (5540 ft.). Trail Area

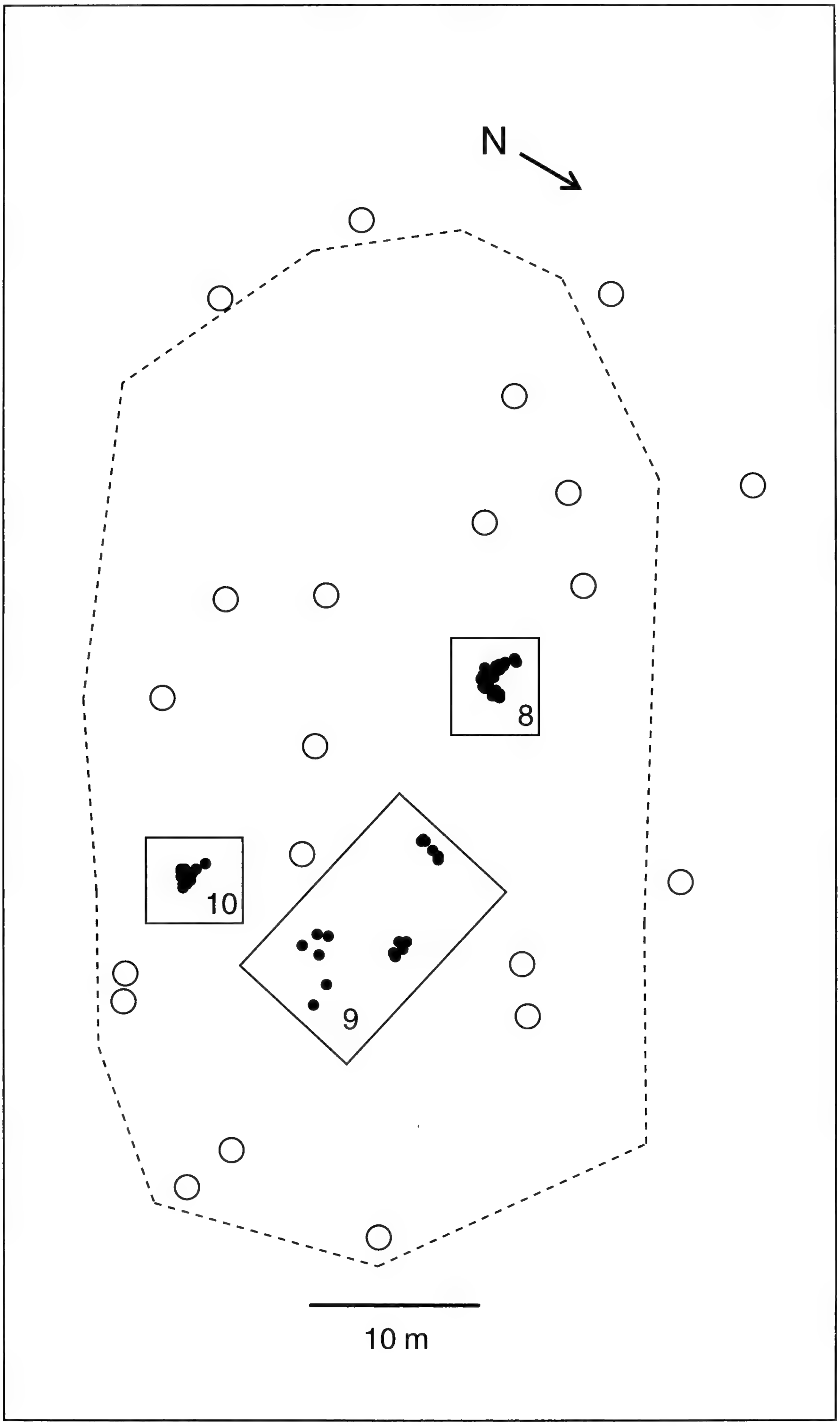

FIG. 1. Map of Trail area including large, established Giant Sequoia (○), seedlings from control burn (●) and burn area boundary (dashed line). Subareas are identified as numbered rectangles but do not represent the physical boundaries for each subarea.

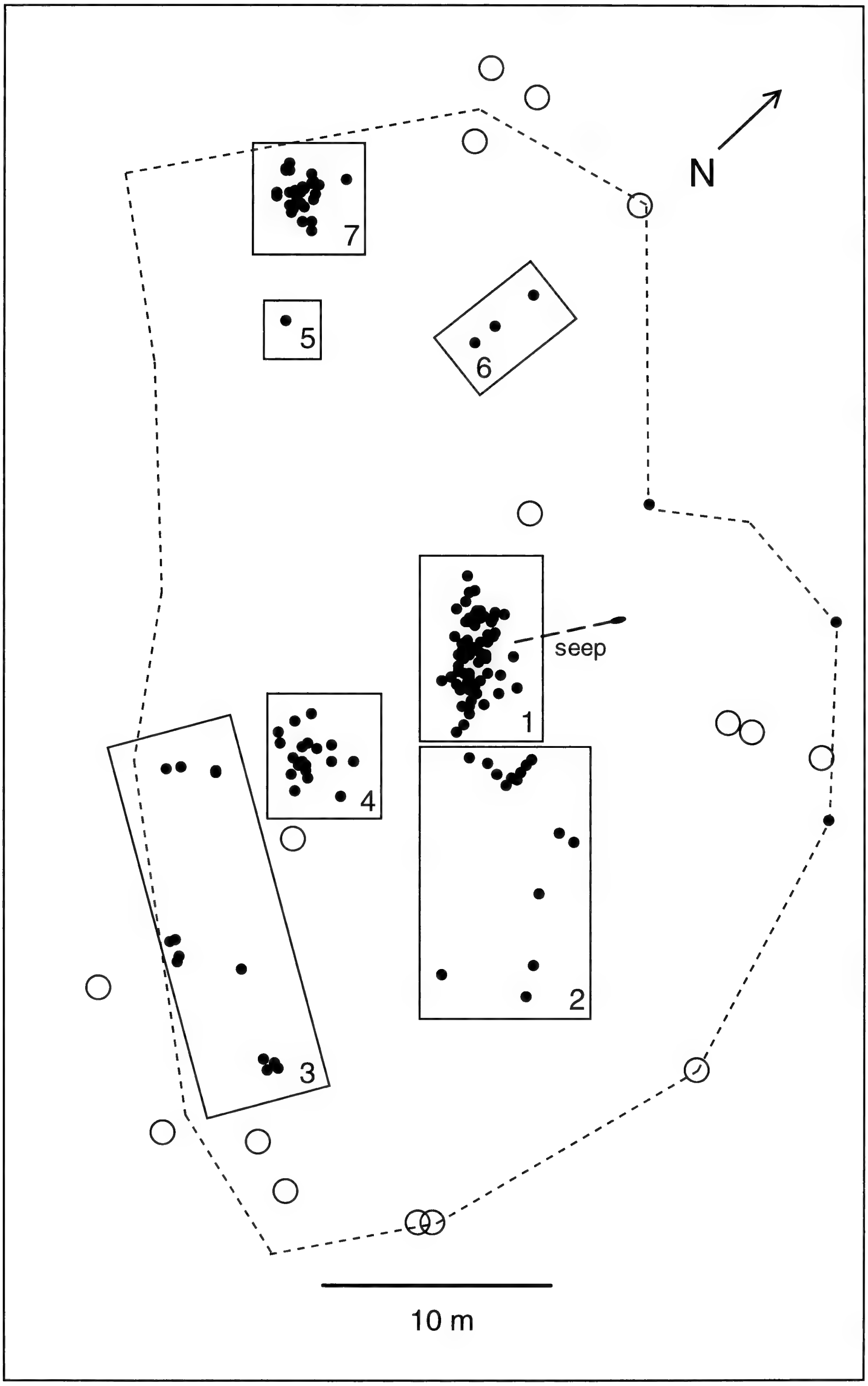

FIG. 2. Map of South area including large, established Giant Sequoia (○), seedlings from control burn (●) and burn area boundary (dashed line). Subareas are identified as numbered rectangles but do not represent the physical boundaries for each subarea.

TABLE 1. CHARACTERISTICS OF SUBAREAS WITHIN SOUTH AND TRAIL AREAS. Rankings for average moisture and average light are from highest (1) to lowest (10) 10% subdivisions. Proximity to nearest mature giant sequoias; Far ≥ 8 m, Close ≤ 4 m, and Mixed = trees scattered at various distances to nearest large trees.

Area	Subarea	Treatment	No. of seedlings	Density	Moisture rank	Light rank	Proximity to big trees
South	1	burn pile	69	dense	1	7	far
South	2	mixed	15	scattered	3	5	far
South	3	non-burn pile	13	scattered	4	6	mixed
South	4	burn pile	19	mixed	5	4	close
South	5	burn pile	1	1 tree	7	1	far
South	6	burn pile	3	3 trees	9	3	far
South	7	non-burn pile	36	dense	2	8	far
Trail	8	burned	42	dense	8	9	far
Trail	9	mixed	17	scattered	6	2	far
Trail	10	mixed	18	scattered	10	10	mixed

faces east, has a 17° degree slope and is moderately rocky. South Area faces west and is generally level with 10° degree or less slopes on one quarter of the site. It has few rocks in its soil. The soil in both areas is a gray-brown podzolic type with a texture varying between fine sand and sandy loam (Harvey et al. 1980).

The two areas had heavy accumulations of downed fuel in the 1960s hence logs and felled snags were cut into sections, piled and burned (producing a burn pile substrate) in Trail Area in 1965 and in South Area in 1966; temperatures beneath the burn piles reached 600° F from 2.5 to 7.5 cm below the surface of the soil (Hartesveldt and Harvey 1967). Bare mineral soil (i.e., scarified substrate) was exposed in some portions of the two areas by the heavy equipment used to move the logs. Other surfaces (i.e., burned substrate) within the areas supported enough fuel to carry surface fires and a few areas supported a mix of scarified and burned substrates.

A total of 7015 seedlings were identified and tagged in Trail and South Areas and monitored at various times over the last four decades (Harvey et al. 1980; Harvey and Shellhammer 1991). These individuals (many now sizable trees) were located in mid-July 2000, measured for height and their precise locations mapped using ultrasonic distance finders (SONIN Combo Pro, SONIN Inc., White Plains, NY) and a triangulation technique (Quigley and Slater 1994). Soil moisture readings as measures of capacitance were taken at 65 to 75 cm depths and from 30 to 60 cm from the base of each individual using a Model 200 Aquaterr Moisture Meter during the middle of summer on July 17th and 18th, 2000. The readings in percent soil moisture were taken in each area on consecutive days to gain an idea of the relative differences in soil moisture between trees and areas during the middle of the summer. Light levels were measured using a Li-Cor 250 light meter. Measurements were taken at the top of smaller individuals and at 2 m above ground level on taller individual trees. Light measurements were performed eight times on one day (hourly between 9 a.m. and 4 p.m.) for each area, the two areas being monitored on consecutive days (July 23rd and 24th) when skies were cloudless. Light intensity readings (in μmols s^{-1} m^{-2}) were summed over the 8-hour period and used to compare the relative differences in light between trees and areas. Finally, three line transects were run across each area between randomly selected mature giant sequoias at the edges of the treatment areas; South Area was monitored on July 18th and Trail on July 28th, 2000. Plant species or wood and bark were identified and measured for height or other parameters at one-meter intervals. Mature giant sequoias (with a diameter at breast height (dbh) ≥2 m) within the areas have long been identified and were located as part of the seedling survey, as were intermediate size giant sequoias (less than 0.3 m dbh) that existed before the experimental burns. No giant sequoias with dbh less the 2 m and more than 0.3 m were present. Coniferous trees of other species were either shrub level trees of 4 m or less in height or larger trees with dbh of 0.3 m or greater and heights of greater than 33 m. The former, shorter trees were included in the line transects while the latter, taller trees were counted but not individually located by survey.

Because their numbers were so small, we combined the individuals derived from all treatments other than "burn pile" (i.e., scarified substrates, burned substrates, and mixed scarified and burned substrates) and categorized them as being "non-burn pile" substrates. Individuals in South and Trail Areas were grouped into "subareas", numbered 1 through 10, based not on physical boundaries but on their pattern of distribution, amount of shade, and treatment, i.e., burn pile or non-burn pile (Table 1, Figs. 1 and 2). Trail Area, for example, was divided into three subareas, two of which had tightly-clumped burn-pile individuals (Subarea 10 was heavily shaded by an over-story of bushes and Subarea 8 was low in moisture and had moderate light)

TABLE 2. DESCRIPTIVE STATISTICS OF TRAIL AND SOUTH AREAS. Means with the same superscript are not significantly different at $\alpha = 0.05$. Light measurements are based on the total of eight measurements taken in one day.

Area	N	Height (cm)		Moisture (%)		Light (µmols s^{-1} m^{-2})	
		Mean	St. Dev.	Mean	St. Dev.	Mean	St. Dev.
Trail	77	208^{a}	186	26^{a}	12	3369^{a}	2467
South	156	356^{b}	228	52^{b}	15	3741^{a}	1988

while the third subarea (Subarea 9) included the rest of the trees, mostly non-burn pile individuals in Trail Area which were more widely distributed in more open conditions. Subarea and burn pile versus non-burn pile designations for each individual facilitated comparisons within and between treatment areas and among subareas. Subareas 6 (three survivors) and 7 were excluded from further analysis due to undetermined effects of a management fire that burned into those subareas (circa 1985) as well as the one tree that made up Subarea 5 (because of its small sample size); those exclusions reduced the total number of trees used in the analysis by 17% (40 of 233 individuals).

Descriptive statistics were performed on measured variables (height, moisture, and light) for trees within areas and subareas using Excel software (Microsoft 2002). Analysis of variance, examining area, subarea, and burnpile effects on tree height, was performed using SAS software (2001). In instances where significant treatment effects occurred, a Tukey's Studentized Range test ($\alpha = 0.05$) was used to compare the differences among these treatments. Correlations and multiple linear regressions were performed on measured variables using SAS software. Soil surface treatment categorical data was assigned a value of 1 for burn pile and 0 for non-burn pile. Correlations and regressions were run twice, once when analyzing subareas 1 through 4 and 8 through 10 (Table 4a) and then also excluding Subarea 1 (Table 4b). We chose to remove Subarea 1 for part of our analyses because it was much moister than the soil moisture conditions common to most giant sequoia groves and hence we did not think it was representative.

RESULTS

The survival success for seedlings in burn piles in South Area (from 1967 through 2000) was 26% (80 of 312) vs. 3% for non-burn pile treatments (51 of 1561); in Trail Area, the survival percentage was 13% (50 of 377) vs. 0% (24 of 4765) for burn pile and non-burn pile treatments. When South and Trail are combined the average survival percentages for burn pile seedlings is 19% as compared with 1% for non-burn pile seedlings, hence giant sequoia seedlings that grew and survived from 1966–67 to 2000 in burn pile substrates had nearly seven times greater survival percentage than those on all other substrates.

South Area was significantly moister than Trail (average soil moisture of 52% vs. 26%, $p < 0.05$) and had the most overall sunlight (3741 vs. 3369 µmols s^{-1} m^{-2}) based on midsummer measurements (Table 2). The average height of seedlings in South was significantly greater than those in Trail (356 cm vs. 208 cm, $p < 0.05$, $n = 231$, t-test). The average height of the 10 tallest trees in both areas (8 in South and 2 in Trail) was 876 cm; they had an average growth rate of 25 cm per year. In contrast the ten shortest trees in the two areas averaged 51.6 cm in height and had an average growth rate of approximately 1.47 cm per year.

When examining differences among subareas it is important to note that the midsummer soil moisture in Subarea 1 (the large group of trees growing near a seep in South Area) was significantly greater than and Subarea 10 (the suppressed group of very short individuals in Trail Area) was significantly lower than all other subareas ($p < 0.05$, $n = 7$, Tukey's Studentized Range test) while midsummer light levels of various subareas were not significantly different from one another due to the large sunlight variance within each subarea (Table 3). Trees in subareas 1 (near a seep), 4 and 9 (in strong sun) were significantly taller ($p < 0.05$, $n = 7$, Tukey's Studentized Range test) than the trees in the other subareas. Subarea 1 had the highest average midsummer soil moisture while Subarea 9 had the highest average midsummer light.

Initial multiple regression analysis indicated that light and surface treatment were highly significant to tree height. This analysis also indicated a significant moisture × surface treatment interaction. Reanalysis within each surface treatment category (burnpile verus non-burnpile) reaffirmed the importance of light and revealed the interplay between moisture and light. When including Subarea 1 (the area with the significantly highest moisture) in the analyses, light and moisture are individually important for trees in burnpile treatments (Table 4a). This result was affected greatly by the large numbers of trees in the wet, burnpile group identified as Subarea 1. The analysis of all non-burnpile trees revealed significant effects of both moisture and a moisture × light interaction on tree height. When trees were analyzed without those in Subarea 1

TABLE 3. MEANS COMPARISONS AMONG SUBAREAS. Means with the same superscript are not significantly different from each other at $\alpha = 0.05$.

Subarea	N	Height (cm)		Moisture (%)		Light (μmols s^{-1} m^{-2})	
		Mean	St. Dev.	Mean	St. Dev.	Mean	St. Dev.
1	69	$463^{a,b,c}$	240	63^{a}	11	$3329^{b,c,d,e,f,g,h}$	1934
2	15	$173^{c,d,e,f,g}$	118	$45^{b,c,d,e,f}$	11	$4553^{a,b,c,d,e,f,g}$	2038
3	13	$138^{d,e,f,g,h}$	66	$39^{b,c,d,e,f}$	6	$4119^{a,b,c,d,e,f,g,h}$	2423
4	19	$341^{a,b,c,d,e}$	200	$38^{c,d,e,f}$	8	$4874^{a,b,c,d,e,f}$	1544
7	36	$314^{b,c,d,e}$	162	$48^{b,c,d}$	12	$3211^{b,c,d,e,f,g,h}$	1657
8	42	$149^{e,f,g,h}$	94	$28^{f,g}$	11	$2921^{c,d,e,f,g,h}$	2320
9	17	$438^{a,b,c,d}$	261	$35^{c,d,e,f,g}$	11	$5787^{a,b,c,d}$	2223
10	18	$127^{e,f,g,h}$	40	12^{h}	3	$2132^{d,e,f,g,h}$	1268

(Table 4b) light was the single determinant of tree height in the burnpiles. In both analyses, none of the selected variables were highly correlated with each other ($r < 0.85$).

Both Trail and South Areas have become crowded with surface litter, plants and an extensive subcanopy of shrubs and small trees (Table 5). Almost 50% of South is covered with shrubs and small trees averaging 2.1 m in height while Trail has 49% cover averaging 3.2 m. Fifteen and 12% respectively of the surfaces of South and Trail are covered by downed wood and bark.

DISCUSSION

The value of heavily burned soil to giant sequoia seedling survival has increased with time (Hartesveldt et al. 1975; Harvey et al. 1980; Harvey and Shellhammer 1991, and present paper for studies in 2000). The proportion of individuals surviving in burn piles compared to those surviving in all of the treatments has grown from 2.5 to 3.5 times greater in 1990 (Harvey and Shellhammer 1991) to nearly 7 times (6.78 times) greater in 2000. Heated soils in giant sequoia groves can be more wettable and friable after intense heating (Donaghey 1969) and it is likely that heating kills seeds of competing species and pathogens in the soil (Harvey and Shellhammer 1991). Those benefits appear to continue in to the first few decades of the seedlings' lives as burn pile individuals were significantly taller than non-burn pile individuals ($p < 0.05$) after 34 to 35 yr, particularly those with higher soil moisture and/or light.

Trail Area had more initial seedlings (5142 versus 1873 for South Area) but had a poorer

TABLE 4. MULTIPLE LINEAR REGRESSION PARAMETERS PREDICTING SEEDLING HEIGHT.

4a. Analysis of subareas 1–4, 8–10

Variable	Estimate	Standard Error	t value	Significance
		Across all burnpile trees		
Intercept	3.785	0.204	18.53	<0.001
Light	0.020	0.006	3.34	0.001
Moisture	0.026	0.004	6.22	<0.001
Moisture × light	-9.3×10^{-5}	1.2×10^{-4}	−0.78	0.438
		Across all non-burnpile trees		
Intercept	5.045	0.420	12.33	<0.001
Light	−0.004	0.014	−0.31	0.759
Moisture	−0.034	0.013	−2.48	0.018
Moisture × light	8.6×10^{-4}	4.1×10^{-4}	2.06	0.046

4b. Analysis of subareas 2–4, 8–10 (excluding Subarea 1)

Variable	Estimate	Standard Error	t value	Significance
		Across all burnpile trees		
Intercept	4.155	0.274	15.13	<0.001
Light	0.019	0.007	2.71	0.008
Moisture	0.007	0.009	0.73	0.468
Moisture × light	4.0×10^{-5}	2.0×10^{-4}	0.20	0.839
		Across all non-burnpile trees		
Intercept	5.045	0.420	12.33	<0.001
Light	−0.004	0.014	−0.31	0.759
Moisture	−0.034	0.013	−2.48	0.018
Moisture × light	8.6×10^{-4}	4.1×10^{-4}	2.06	0.046

TABLE 5. GROUND, SHRUB AND SMALL TREE COVER BY AREA. Nomenclature follows Hickman (1993).

5.a Ground cover

South Area % cover	Species	Trail Area % cover
36.53	litter, duff	41.64
20.33	*Rubus* spp.	4.49
16.10	downed wood/bark	11.87
8.49	*Lupinus latifolius*	13.08
4.90	*Castilleja disticha*	<1.00
3.50	*Clintonia uniflora*	5.67
0.00	*Galium sparsiflorum*	3.15
2.61	*Rosa californica*	2.15
0.00	Rock	2.60
0.00	*Castilleja* spp.	2.15
1.99	*Adenocaulon bicolor*	6.80
1.78	*Potentilla glandulosa*	<1.00
1.10	*Disporum trachyandrum*	1.82
1.01	*Hieracium albiflorum*	<1.00
<1.66	13 other species	<1.58

5.b Downed wood/bark

South Area % cover	Condition	Trail Area % cover
1.99	Sound, <0.6 m	1.33
2.26	Sound, >0.6 m	0.39
1.42	Rotten, <0.6 m	4.49
8.69	Rotten, >0.6 m	3.80
0.74	Bark	1.90

5.c Shrub/small tree subcanopy

South Area % cover	Height (m)	Species	Trail Area % cover	Height (m)
15.46	0.9	*Ceanothus parvifolius*	2.08	3.0
12.58	3.9	*Abies concolor*	15.03	3.6
10.09	0.9	ferns	0.00	0.0
7.84	3.1	*Ceanothus integerrimus*	8.13	4.4
1.55	4.4	*Cornus nuttallii*	14.59	2.1
1.28	0.9	*Ribes cereum*	0.74	1.2
0.95	0.6	*Ribes roezlii*	0.54	1.4
0.00	0.0	*Calocedrus decurrens*	6.26	2.6
0.00	0.0	*Pinus lambertiana*	0.62	7.6
0.00	0.0	*Sequoiadendron*	0.08	1.1
Total 49.75%	Average 2.1		Total 48.75%	Average 3.2

survival rate for both burn pile and non-burn pile seedlings, primarily because of significantly less soil moisture in burn pile areas (i.e., Subareas 8 and 10) and less moisture and heavy overtopping by shrubs and small trees (Subarea 8); these two subareas, that had the shortest individuals, had the least soil moisture and the least light of any of the 10 subareas (Table 3).

Assuming it is reasonable to extrapolate from the mid-summer moisture and light measurements to longer periods of time, it appears that the moisture-light interaction is likely to be more important in the early years of growth (i.e., without enough soil moisture or light seedlings die) and that light generally becomes more important after that except in areas of high soil moisture, such as Subarea 1 in South where the tallest trees are growing in slightly below average light. After desiccation and insect damage killed most seedlings in both areas in their first and second years (Harvey et al. 1980) many of the individuals that survived have grown well in conditions ranging from relatively low moisture and high light (as in Subarea 9) to high moisture and relatively low light (as in Subarea 1). When both moisture and light are low, as in Subarea 8 in Trail Area, height has been greatly reduced. The seedlings that have generally grown the tallest, however, were trees (in Subarea 9 in Trail Area) growing more or less equidistant from mature trees where we assume they have experienced less root competition and have received relatively high amounts of light. In this context, our results agree in part with those of (Demetry 1995) who found that the taller seedlings, and later young trees, were at gap centers where there was less root competition. She found that the height of seedling in gaps was associated

with water availability whereas we found that the tall individuals living in naturally-occurring gaps (e.g., those in Subarea 9) were experiencing high light levels and only moderate moisture compared to other trees in this study. Light is very important when seedlings are found in crowded conditions, as were found in the moist Subarea 1. Less light is partially compensated for by high moisture is very moist areas but high light is necessary for continued growth as we found some of our tallest trees in areas of high light and modest to low moisture. The impact of the burnpile treatment is clearly evident in the number and vigor of the survivors. For this treatment, light is the key player in determining tree height. In the non-burnpile treatments, the interaction of light with moisture is important. For the smallest trees in these treatments, light is the limiting agent irregardless of moisture. On the other hand, the tallest trees have high light and at least modest moisture.

The fact that the tallest trees in our study are growing in areas relatively far from mature giant sequoias is partially the result of the burn pile placement. Burn piles were interspaced between mature trees so as not to heat kill or damage the big trees; the 1965 and 1966 burns, after all, were the first experimental use of fire in a western national park and it appears in retrospect that we were overly careful to avoid heat damage to the mature sequoias. Five of the tallest individuals, however, (including the 4th and 7th tallest) are non-burn pile trees in Subarea 9 in Trail Area. These trees are growing in high light and moderate to low moisture conditions are usually equidistant and relatively far away from the nearest mature giant sequoias. In this general area, desiccation and later root competition from the big trees is likely to have killed off the hundreds of seedlings that originally germinated between them and the nearest big trees. The tree we identify as being the only individual in Subarea 5 (Table 3, Fig. 2) was the 8th tallest tree in the study and was growing in an area of very high light and low soil moisture and was located away from mature giant sequoias. In contrast, individuals in Subarea 8 (in Trail Area) are a few meters from a small seep arising between several big trees upslope of them but they did not benefit from it. They are within the root zone of the nearest giant sequoia and that may partially account for the low soil moisture in that subarea. The low moisture plus their density and associated competition appears to account for their low average height. It seems apparent to us that while soil moisture and light are necessary for germination and establishment, recruitment (i.e., individuals that have grown into trees of reproductive age) is more dependent on abundant light and to some degree distance from preexisting mature trees than soil moisture alone.

The assignment of subareas was based on soil surface treatment at the time of the burn (1965 & 1966) in addition to the resultant pattern of tree distribution (2000). In this manner, true replication of subarea conditions was not possible. Pseudoreplication issues such as this, while acknowledged by the authors (Hurlbert 1984) as common to fire ecology research, do not preclude us from drawing conclusions about the effects of light and moisture on survivor vigor. Extrapolation of the effects such as fire intensity (as manipulated via the burn piles) to areas outside research plots should be approached with caution.

Trail and South Areas have not experienced fire since 1965 and 1966 respectively (with the exception of a nearby management burn that burnt into the corner of South Area near Subarea 7). The buildup of fuel in the two areas (Table 5) reflects a long inter-fire interval, an interval that far exceeds the 2–10 yr "natural" fire interval suggested by Kilgore and Taylor (1979), Swetnam (1993) and Swetnam et al. (1992) for low to moderate intensity fires or the 10–35 yr interval suggested by Kilgore and (Talyor 1979) for low intensity fires with patchy high intensity. There was such a heavy fuel load of downed logs and dead snags in Trail and South Areas in the mid - 1960's that we created burn piles to avoid creating conditions hot enough to heavily scorch large trees or start crown fires. Because we used burn piles in this manner we created relatively low intensity surface burns in the other parts of the study areas, which in turn did not heat kill many of the intermediate-sized white firs as has been the case in prescribed fires carried out in Sequoia and Kings Canyon National Parks since the time of our study; the Park prescribed fires typically have been hotter than ours were and have better reduced the stands density of white firs (*Abies concolor*) as well as total fuel loads (Keifer 1998). Our fires were hot enough to create a heavy seed fall and to remove surface litter and vegetation, and hence allow for germination, but not hot enough to open up the canopy. Our "hot spots" therefore were much smaller than those described by Kilgore and Taylor (1979), and discussed further by Stephenson (1994), for low intensity fires with patches of higher intensity.

As of the year 2000, both South and Trail Areas were approaching a "ladder type" forest structure as it pertains to fire, with abundant downed wood, a thick layer (or subcanopy) of shrubs and small trees and an intermediate subcanopy of white firs and incense cedars that have the potential to carry future fires into the lower branches and hence into the crowns of the mature trees in these areas. Two, or likely more, fire intervals under natural conditions (Kilgore and

Taylor 1997; Swetnam 1993; Swetnam et al. 1992) have passed since the inception of this study. The amount of surface and subcanopy vegetation that has built up from what was essentially bare and burned mineral soil in 1965 and 1966 provides all those who observe these areas with a graphic reminder of not only the role of fire in the regeneration of giant sequoia groves but also the problems that arise when frequent fires are excluded from them. Our study, and those of others (Kilgore and Taylor 1997; Swetnam 1993; Swetnam et al. 1992), indicate that controlled burns need to be applied to the groves on a regular basis to set back succession, promote continued regeneration of giant sequoias and protect the groves from destructive crown fires.

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PHYTOLITH EVIDENCE FOR THE LACK OF A GRASS UNDERSTORY IN A *SEQUOIADENDRON GIGANTEUM* (TAXODIACEAE) STAND IN THE CENTRAL SIERRA NEVADA, CALIFORNIA

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ABSTRACT

Tree ring fire-scars in *Sequoiadendron giganteum* (giant sequoia) stands record a high frequency, low intensity, prehistoric fire regime. Difficulties achieving short prehistoric fire return intervals with prescribed burns at a *S. giganteum* stand in Calaveras Big Trees State Park, California, currently characterized by dense tree cover with little understory vegetation due to over a century of fire suppression, suggest that a prehistoric grass understory provided fine fuel required for frequent fire spread. We used phytolith analysis to test this hypothesis. Phytoliths, microscopic silica bodies found in many plants but produced in large quantities with distinctive morphotypes in grasses, are preserved for thousands of years in the soil. Soils under vegetation with extensive prehistoric grass cover retain a high concentration of grass phytoliths regardless of historic vegetation changes. Phytoliths were extracted from soil samples taken from pits dug at 14 plots throughout a *S. giganteum* stand in the South Grove Natural Preserve. Soil phytolith weight for most plots, currently without grass cover and comprising most of the stand, was less than 0.10%, consistent with reported values for forests with no grass in the understory. Soil phytolith weights for ridge-top plots and plots near the stream channel were significantly higher, suggesting localized areas with sparse grass cover. The hypothesis that there was substantial prehistoric grass cover in this *S. giganteum* stand was rejected.

Key Words: *Sequoiadendron giganteum*, giant sequoia, phytoliths, fire regime, California grasses, California paleoecology, Sierra Nevada, Calaveras Big Trees.

Fire is an important ecosystem process in *Sequoiadendron giganteum* (Lindley) Buchholz (giant sequoia) stands in the central Sierra Nevada in California. *Sequoia giganteum* appears to be dependent upon ground fires for regeneration in many areas. Cones open following fire to release seeds; a few years following ground fire, newly germinated *S. giganteum* seedlings dominate burned areas (Kilgore 1973; Parsons and DeBenedetti 1979; Mutch and Swetnam 1995). Analyses of tree-ring fire-scars from living trees and stumps in the Sierra Nevada indicate that prior to the mid-1800s there was a composite mean fire return interval of approximately five years in *S. giganteum* stands of the mixed-conifer forest type (Swetnam 1993; Caprio and Swetnam 1995; Parsons 1995). This means that tree-ring fire-scars recorded a surface fire somewhere within the sampling area (ranging from 13 to 69 ha [Swetnam 1993]) every five years, averaged over a period of 2000 yr, with considerable variability at the decadal and centennial scales and between groves (Swetnam et al. 1992). These

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surface fires occurred in a patchy, mosaic pattern, and because crown fires involving *S. giganteum* were evidently rare (judging from the presence of trees in excess of 1500 yr old), caused little mortality to large trees. Frequent, low intensity ground fires were probably important for forest health and maintained *S. giganteum* groves in open, park-like stands.

From about 1860 to 1900, natural ecosystem processes in *S. giganteum* stands, including fire, were drastically altered by livestock grazing (mainly sheep), cessation of aboriginal burning practices, limited logging, and suppression of natural or human-caused wildfires (Kilgore and Taylor 1979). Currently, many mixed conifer forest stands at Calaveras Big Trees State Park are thickets of mid-sized trees, often dominated by *Abies concolor* (Gordon and Glend.) Lindley (white fir) and *Calocedrus decurrens* (Torrey) Florin (incense cedar). There is little understory vegetation because the overstory canopy is almost closed and provides little opportunity for light to reach the forest floor. The conditions wherein *S. giganteum* stands can self-perpetuate and flourish no longer exist.

Based on tree-ring analysis, from 500 AD to 1900 AD, the longest recorded period without a fire in a *S. giganteum* stand was approximately 60 yr, while during centuries with high fire frequencies (generally periods of drought) the longest non-burn interval per stand was typically no more than 13 yr (Swetnam 1993). There are currently some *S. giganteum* stands that have had no fire for the past 100 yr.

Prescribed fire has been introduced into *S. giganteum* stands in many parks in the Sierra Nevada, including Calaveras Big Trees State Park, as a means of restoring more natural conditions. Ground fires have typically been set under proper conditions in late summer or fall with goals of removing excessive fuels, killing invading *A. concolor* and *C. decurrens* trees, and restoring natural processes. Experience at Calaveras Big Trees State Park has revealed that for up to 15 yr following initial prescribed burning, the understory vegetation and overstory canopy conditions will not support extensive surface fires. Maintaining a mean fire return interval of five years has not been possible because not enough fuel is available to adequately carry surface fire throughout *S. giganteum* stands. To approach the relatively short mean fire return interval suggested by the tree-ring fire-scar evidence, it appears there may have been different overstory species, such as deciduous hardwoods, contributing fuel to the forest floor, or understory shrubs, herbs, or grasses that grew more densely and provided fuel for frequent fires.

The precise structure of pre-1850 *S. giganteum* stands, particularly the composition and biomass of understory plant species, is unknown (Vankat and Major 1978; Stephenson 1996; Stephenson 1999). In the 1860s, livestock grazing, principally large flocks of sheep, was introduced into the central Sierra Nevada (Swetnam 1993; Kilgore and Taylor 1979), suggesting there was a substantial amount of forage available. Researchers in many areas of the western United States, particularly the monsoonal southwest, have found that fine fuels, especially grasses, were important for the spread of ground fires. The removal of these fuels through overgrazing by livestock beginning in the mid-1800s probably led to sharp declines in fire frequency (Swetnam et al. 1991; Caprio and Lineback 2002).

Prior to alteration of natural fire regimes in the mid-1800s, *S. giganteum* and mixed conifer stands in the vicinity of Calaveras Big Trees State Park were probably composed of widely spaced, large diameter, towering *S. giganteum*, a few *Pinus lambertiana* Douglas (sugar pine) and *Pinus ponderosa* Laws. (ponderosa pine), and a lesser element of *A. concolor* and *C. decurrens*. These stands were probably devoid of dense woody understory vegetation because of frequent surface fires ignited by native people or lightning. The open nature of these stands may have allowed sufficient sunlight to reach the forest floor to support an extensive understory of native grass species, which during the dry season served to carry frequent surface fires throughout the forest stand (e.g., Swetnam et al. 1992). These surface fires would have killed most small shrubs and trees, removed smothering duff layers, recycled nutrients, perpetuated the grass-dominated understory vegetation, and maintained gaps in the stands for forest regeneration. Unfortunately, little solid evidence exists either way regarding the existence of this prehistoric grass understory.

We used phytolith analysis to test the hypothesis that grasses were an important prehistoric component of the understory of *S. giganteum* stands. Opal phytoliths are microscopic particles of silica formed in the cells of many plants and released into the soil during decomposition (Piperno 2006). Phytoliths are highly resistant to weathering and in many soil environments will persist for thousands or even millions of years (Wilding 1967; Strömberg 2004). Grasses produce many more phytoliths than most other plant taxa, averaging 3% and commonly ranging from 1–5% dry weight phytolith content (Witty and Knox 1964; Piperno 2006). Most conifer species produce <0.5% dry weight phytolith content (Klein and Geis 1978; Hodson et al. 1997). Consequently, soils formed under grassland vegetation contain an order of magnitude more phytoliths (1–3%) than soils formed under forest vegetation with few grasses (Witty and Knox 1964; Jones and Beavers 1964; Wilding and Drees 1968; Norgren 1973; Miles and Singleton 1975).

Phytoliths often take the shape of the cell in which they are formed. Most phytolith shapes are produced by many different plant taxa, but a few taxa produce distinctive phytolith morphotypes (Rovner 1971). Grasses produce short cell phytoliths in specialized silica accumulator cells that are diagnostic of the Poaceae family. Short cell phytoliths, including rondels, bilobates, and saddles, have been used to identify grasses to the subfamily level (Twiss et al. 1969; Twiss 1992; Mulholland and Rapp 1992).

Several studies have used soil phytoliths to document changes in dominant vegetation over time. In the prairie peninsula in Illinois, Wilding and Drees (1968) used differences in soil phytolith content (measured as percent dry weight) to identify areas of prehistoric forest, grassland, and the forest-grassland ecotone. In Utah, Fisher et al. (1995) used changes in phytolith morphotype percentages in the soil profile to document a shift from grassland to shrubland with the introduction of grazing. Bartolome et al. (1986), working at Jepson Prairie in the California Central Valley, used changes in the concentration of bilobate grass phytolith shapes with soil depth to infer a prehistoric shift from *Nassella*-dominated perennial grassland to the exotic annual grassland present today. Bicknell et al. (1992, 1993) used soil phytolith concentration to map the extent of prehistoric grasslands at several state parks in coastal California, finding many currently forested areas were grasslands prior to European settlement and many current grasslands were previously forested. In northern Arizona, the percent dry weight of phytoliths in the soil and the relative percent of morphotypes in the soil phytolith assemblage were analyzed for a *P. ponderosa* forest with a bunchgrass understory to determine the long-term stability of the current vegetation (Kerns 1999, 2001; Kerns et al. 2001, 2003). High concentrations of pine and grass phytoliths in soil surface and subsurface samples indicated little change over time. All of these studies have indicated that if there was substantial prehistoric grass cover on a site, there will be a high concentration of grass phytoliths in the soil.

METHODS

Site Description

The study area is located in the South Grove Natural Preserve of Calaveras Big Trees State Park, 200 km east of Stockton, California (Fig. 1). The park is 2625 ha with an elevation range from 1000 m to 1700 m. Topography is dissected, with a western slope overall, and NE-SW trending ridges between steep river canyons. The climate of the western Sierra Nevada is distinctly seasonal and highly influenced by elevation. The annual precipitation at the elevation of the park ranges from 100 to 170 cm, much of it coming as snow; about 90% of the total precipitation occurs during the six month period between November and April (Walfoort and Hunt 1982).

Soils in the South Grove Natural Preserve (Fig. 2) are dominated by the McCarthy series, inceptisols characterized as gravelly sandy loam/very gravelly sandy loam found on slopes of 5 to 60%. Soil pH ranges from 6.3 at the surface to 5.9 at 60 cm depth. Parent material is well-drained, basic, volcanic rock with rapid permeability.

Overstory vegetation at Calaveras Big Trees State Park is largely pine/mixed pine and fir forest dominated by *Pinus ponderosa* (ponderosa pine), *Pinus lambertiana* (sugar pine), and *Abies concolor* (white fir) in either pure or mixed stands. *Calocedrus decurrens* (incense cedar), *Quercus kelloggii* Newb. (California black oak) and *Quercus chrysolepis* Liebm. (canyon live oak) also occur within the park. Vascular plants that have been identified in the park include over 60 families, 159 genera, and 219 species (Walfoort and Hunt 1982). Common species are listed in Table 1.

The *Sequioadendron giganteum* (giant sequoia) stands of the park are located in two groves, designated the North and South Groves. In the never-logged South Grove, *S. giganteum* comprises 65.9% of the total basal area, followed by *A. concolor* at 21.7% (Walfoort and Hunt 1982). Grass cover is very sparse throughout the grove, with maximum 5% cover in patches near the top of the watershed's north ridge.

Phytolith Reference Collection

To better understand the soil phytolith assemblage, a phytolith reference collection, composed of phytoliths extracted from leaf samples from all major plant species currently present in the study area (Table 1), was assembled. Phytoliths were extracted using a modified dry ashing technique (Piperno 2006; Pearsall 2000; Kondo et al. 1994). Samples were washed in distilled water to remove adhering minerals, dried at 60°C and weighed, rinsed in 10% HCl to improve combustion, ashed in a muffle furnace at 550°C for 4 hr, rinsed again in 10% HCl to remove acid-soluble residue, washed 3 times in water, dried in ethanol, and the dry residue weighed. To view phytoliths, dry residue was resuspended in immersion oil so that phytoliths could be rotated and three-dimensional characteristics observed, mounted on a slide, and viewed under a phase-contrast light microscope at 400×. Two slides for each plant were scanned completely and potentially diagnostic phytolith types noted.

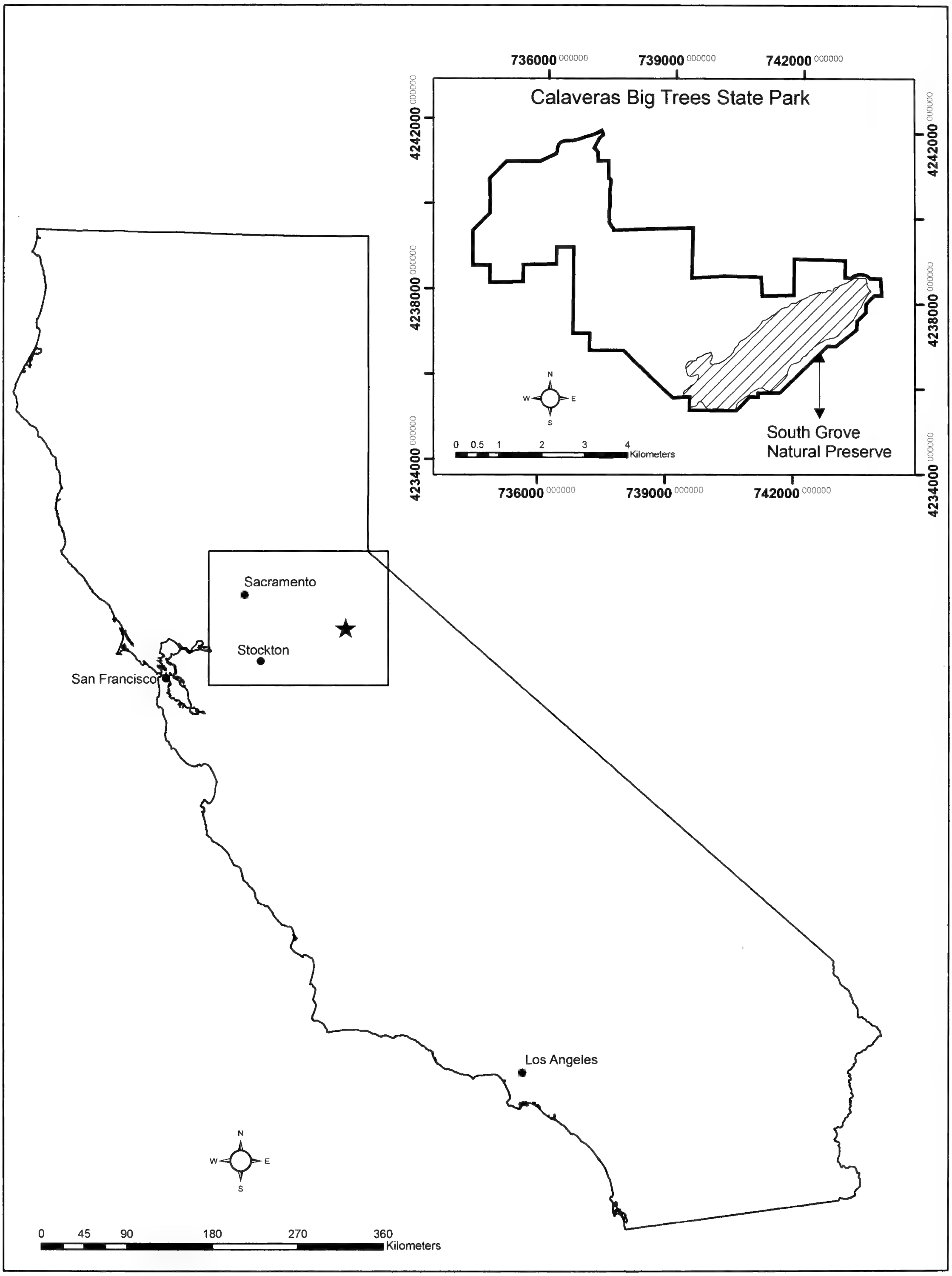

FIG. 1. Location of Calaveras Big Trees State Park and the South Grove Natural Preserve, georeferenced in UTM.

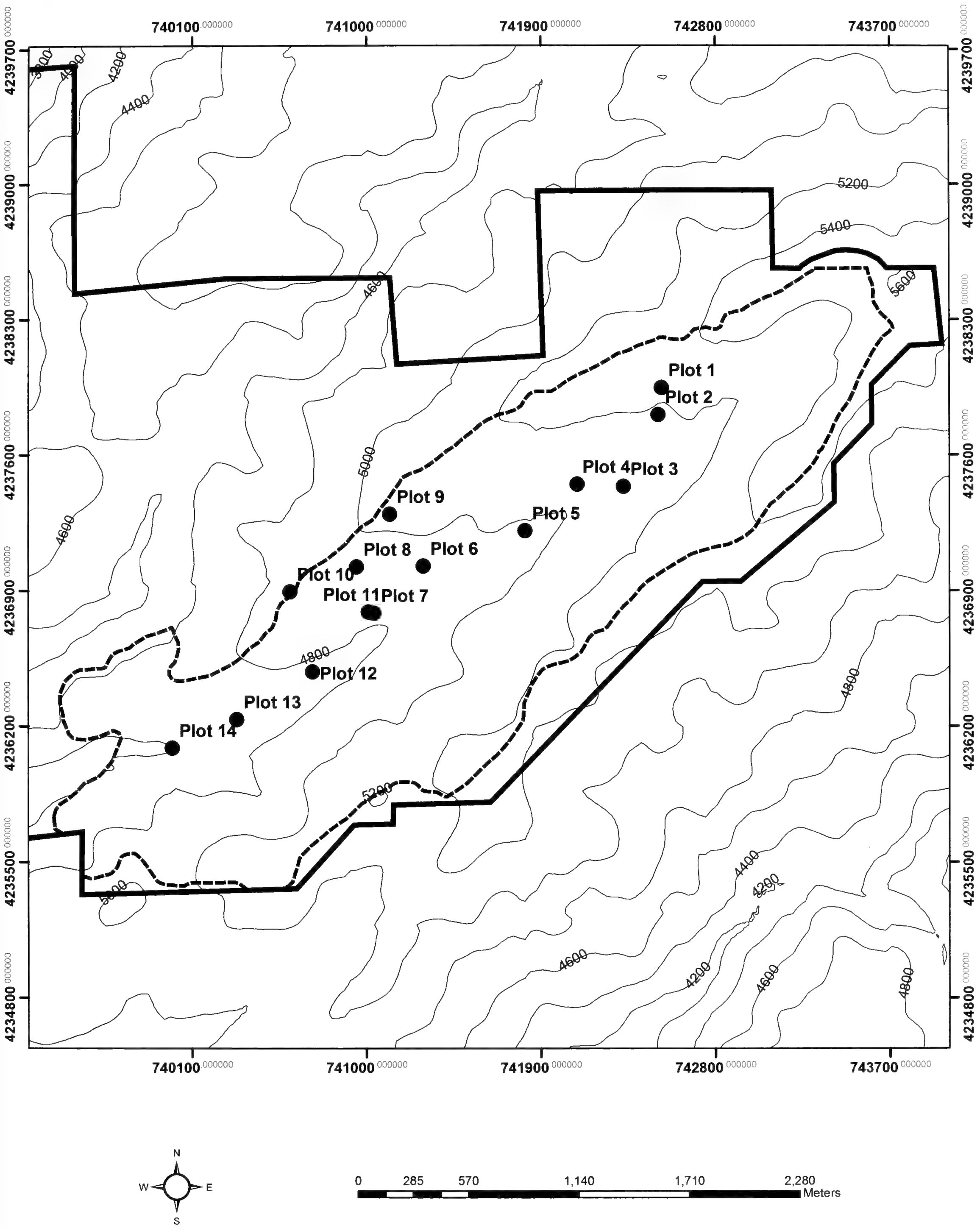

FIG. 2. Location of phytolith sampling plots in the South Grove Natural Preserve, Calaveras Big Trees State Park, georeferenced in UTM.

Soil Phytolith Extraction

Soil samples were collected from soil pits dug on 14 plots (Fig. 2). Plots were selected to span the topographic gradient of the watershed, particularly but not exclusively in locations currently occupied by giant sequoia. To assess within plot variation in soil phytoliths, two pits within 100 m of each other were dug and sampled at each plot. Phytolith samples from both pits

TABLE 1. PLANT SPECIES PRESENT IN CALAVERAS BIG TREES STATE PARK, SAMPLED FOR THE PHYTOLITH REFERENCE COLLECTION, WITH LEAF SILICA PERCENTAGE BY WEIGHT AND OBSERVED DIAGNOSTIC PHYTOLITH MORPHOTYPES.

Species	Family	Common Name	Silica (%)	Diagnostic Morphotypes
Trees				
Abies concolor (Gordon and Glend.) Lindley	Pinaceae	white fir	0.1	none
Acer macorphyllum Pursh	Aceraceae	big-leaf maple	0.5	none
Alnus rhombifolia Nutt.	Betulaceae	white alder	<0.1	none
Calocedrus decurrens (Torrey) Florin	Cupressaceae	incense cedar	<0.1	none
Cornus nuttallii Audubon	Cornaceae	dogwood	<0.1	none
Corylus cornuta Marsh var. californica (A. DC.) W. Sharp	Betulaceae	California hazelnut	0.3	none
Pinus lambertiana Douglas	Pinaceae	sugar pine	<0.1	none
Pinus ponderosa Laws.	Pinaceae	ponderosa pine	0.5	spiny bodies, spiny rods
Pseudotsuga menziesii (Mirbel) Franco var. menziesii	Pinaceae	Douglas-fir	0.4	none
Quercus kelloggii Newb.	Fagaceae	black oak	0.3	none
Sequoiadendron giganteum (Lindley) Buchholz	Taxodiaceae	giant sequoia	0.1	none
Shrubs				
Arctostaphylos patula Greene	Ericaceae	green-leaf manzanita	<0.1	none
Ceanothus cordulatus Kellogg	Rhamnaceae	mountain whitethorn	0.6	none
Ceanothus integerrimus Hook. & Arn.	Rhamnaceae	deer brush	<0.1	none
Chamaebatia foliolosa Benth.	Rosaceae	mountain misery	0.4	none
Chimaphila umbellata (L.) Bartram	Ericaceae	pipsissewa	0.1	none
Chrysolepis sempervirens (Kellogg) Hjelmq.	Fagaceae	bush chinquapin	0.1	none
Rhododendron occidentale (Torrey & A. Gray) A. Gray	Ericaceae	western azalea	<0.1	none
Rosa pinetorum A.A. Heller	Rosaceae	pine rose	0.4	none
Rubus parviflorus Nutt.	Rosaceae	thimbleberry	<0.1	none
Ribes roezlii Regel	Grossulariaceae	Sierra gooseberry	0.2	none
Symphoricarpus mollis Nutt.	Caprifoliaceae	snowberry	<0.1	none
Herbs				
Adenocaulon bicolor Hook.	Asteraceae	trail plant	0.1	none
Aquilegia formosa Fischer	Ranunculaceae	crimson columbine	0.1	none
Asarum hartwegii S. Watson	Aristolochiaceae	wild-ginger	<0.1	none
Carex sp.	Cyperaceae	sedge	4.3	conical cells
Clintonia uniflora (Schultes) Kunth	Liliaceae	bride's bonnet	<0.1	none
Fragaria vesca L.	Rosaceae	wood strawberry	0.2	none
Galium aparine L.	Rubiaceae	goose grass	2.3	none
Hieracium albiflorum Hook.	Asteraceae	hawkweed	0.2	none
Iris hartwegii Baker	Iridaceae	Hartweg's iris	0.2	none
Lonicera involucrata (Richardson) Banks	Caprifoliaceae	twinberry	<0.1	none
Lupinus sp.	Fabaceae	lupine	0.1	none
Phacelia sp.	Hydrophyllaceae	phacelia	0.3	none
Pyrola picta Smith	Ericaceae	white-veined shinleaf	0.1	none
Smilacina racemosa (L.) Link	Liliaceae	false solomon's seal	<0.1	none
Trientalis latifolia Hook.	Primulaceae	starflower	<0.1	none
Viola lobata Benth.	Violaceae	pine violet	<0.1	none
Grasses				short cells, trichomes, bulliforms
Achnatherum lemmonii (Vasey) Barkworth	Poaceae	Lemmon's stipa	5.1	bilobate short cells
Bromus carinatus Hook. & Arn.	Poaceae	California brome	4.5	rondel short cells
Danthonia unispicata (Thurber) Macoun	Poaceae	one-spike oatgrass	1.9	bilobate short cells
Elymus elymoides (Raf.) Swezey	Poaceae	squirreltail	13.5	rondel short cells
Festuca rubra L.	Poaceae	red fescue	3.4	rondel short cells
Melica aristata Bolander	Poaceae	awned melic	3.2	bilobate short cells
Poa secunda J.S. Presl	Poaceae	one-sided bluegrass	6.1	rondel short cells

TABLE 2. SOIL PHYTOLITH WEIGHT AS A PERCENTAGE OF SOIL WEIGHT AND PERCENTAGE OF DIAGNOSTIC GRASS PHYTOLITHS IN SOIL PHYTOLITH ASSEMBLAGE IN RELATION TO SOIL DEPTH AND TOPOGRAPHIC POSITION IN THE SOUTH GROVE NATURAL PRESERVE, CALAVERAS BIG TREES STATE PARK.

Topographic Position	Soil Depth (cm)	Soil Phytolith Weight (%)	95% t-value Confidence Interval	Grass Phytoliths (%)	95% t-value Confidence Interval
Hillside plots (N=9)	Surface	0.08	0.06–0.10	21	14–28
	10	0.04	0.03–0.05	17	12–22
	25	0.02	0.01–0.03	26	17–35
	40	<0.01	—	—	—
	55	<0.01	—	—	—
Ridge-top PIPO plots (N=6)	Surface	0.47	0.35—0.59	12	5–19
	10	0.36	0.24–0.48	12	10–14
	25	0.37	0.25–0.49	15	10–20
	40	0.32	0.15–0.49	11	1–21
	55	0.18	0.00–0.38	15	8–22
Lower channel-side plots (N=4)	Surface	0.31	0.25–0.37	43	37–49
	10	0.52	0.38–0.66	31	20–42
	25	0.53	0.39–0.67	38	30–46
	40	0.44	0.33–0.55	35	18–52
	55	0.43	0.35–0.51	42	28–56

were processed and counted for plots that had >0.10% soil phytoliths; otherwise, samples from only one pit were processed. Soil samples were collected from each pit at five depths, each depth corresponding to a soil horizon because soils were similar throughout the site: mineral soil surface (A horizon), 10 cm (upper B horizon), 25 cm (middle B horizon), 40 cm (lower B horizon), and 55 cm (C horizon). Because the soil horizon generally corresponded with soil depth, soil phytolith data from each plot were aggregated by sample depth, which may be a rough approximation of relative sample age (e.g., Alexandre et al. 1999), for analysis.

Phytoliths were extracted from five gram soil samples by standard procedures: deflocculation in Calgon, HCl wash, organic matter digestion in 30% hydrogen peroxide, two heavy liquid flotations in zinc bromide solution at specific gravity 2.30 (a third flotation for several samples produced negligible additional phytoliths and was deemed unnecessary), and mounted on slides as above (Carbone 1977; Kondo et al. 1994). Because the biogenic silica residue contained diatoms and residual mineral silica particles, phytolith weight for each sample was estimated by examining 10 microscope fields on a slide, estimating the percentage of non-phytolith material, and subtracting this percentage from the measured residue weight (Carnelli et al. 2001). Phytolith morphological types were tallied for each soil sample until 400 total phytoliths were counted. Diagnostic types were tallied individually by taxon. Non-diagnostic types were lumped together; no attempt was made to identify or tally each individual non-diagnostic type. The percentage of diagnostic grass phytoliths (i.e., morphotypes observed in grasses but not observed in other plants in the reference collection, including simple trichomes, bulliforms, three types of long cells, and short cells) out of total phytoliths in each sample was calculated.

RESULTS

Extracted reference material from most plant species contained small amounts of poorly silicified biogenic silica but no diagnostic phytoliths (Table 1). *Pinus ponderosa* was the only tree species with diagnostic phytoliths: spiny bodies and spiny rods (Norgren 1973; Kerns 2001) were isolated from needles. Several tree species produced phytolith morphotypes that were distinct from grasses but not diagnostic beyond this level. No shrubs contained diagnostic phytoliths. *Carex* (sedge) species produced non-diagnostic long cells and diagnostic conical phytoliths (Ollendorf 1992). All grasses contained abundant phytoliths, including long cells, trichomes, bulliforms, and short cells (Twiss et al. 1969; Twiss 1992). *Achnatherum lemmonii* (Vasey) Barkworth, *Danthonia unispicata* (Thurber) Macoun, and *Melica aristata* Bolander were the only grasses sampled producing bilobate short cells. Other grasses produced abundant rondel short cells.

Soil phytolith weight averaged less than 0.55% on all plots (Table 2), but varied according to topographic position in the watershed. Hillside plots (Fig. 2: Plots 1–7, 11, 12), typical of most of the sampled watershed, had very low soil phytolith concentration (<0.10%) at all depths. Plots on or near the ridge (Plots 8–10), where *P. ponderosa* was present in the overstory, contained significantly more soil phytoliths (of which 42% were *P. ponderosa* spiny bodies) at all depths than hillside plots. Plots in the lower part of the

TABLE 3. ESTIMATED PERCENTAGE OF PHYTOLITHS IN THE SOIL BENEATH GRASSLAND AND FOREST VEGETATION FROM STUDY SITES IN NORTH AMERICA.

Location	Vegetation Type	Soil Phytolith (%)	Size Fraction (μ)	Estimation Method	Reference
Alberta	Grassland	0.83–2.78	20–50	particle count	Lutwick and Johnston 1969
Arizona	Ponderosa pine-grassland	0.9–1.4	5–250	dry weight	Kerns et al. 2001
Illinois	Grassland	0.77–1.23	20–50	particle count	Beavers and Stephen 1958
	Hardwood forest	0.19–0.28	20–50	particle count	Beavers and Stephen 1958
Minnesota	Oak forest and grassland	1.54–3.63	5–50	particle count	Verma and Rust 1969
North Carolina	Oak hardwood and grass	0.94–0.99	all	dry weight	Knoepp et al. 1998
Oregon	Ponderosa pine	0.13–0.26	15–100	particle count	Witty and Knox 1964
	Grassland	1.92–2.89	15–100	particle count	Witty and Knox 1964
Pennsylvania	Grassland	1.19–1.75	20–50	dry weight	Waltman and Ciolkosz 1995
	Hardwood forest	0.07–0.33	20–50	dry weight	Waltman and Ciolkosz 1995

watershed within <50 m of the stream channel (Plots 13, 14), where no *P. ponderosa* was observed in the overstory, also contained significantly more soil phytoliths than hillside plots.

All plots contained diagnostic grass phytoliths, but topographic position influenced grass phytolith percentages (Table 2). Hillside plots had the lowest percentage of grass phytoliths; channel-side plots had significantly more grass phytoliths than either of the other topographic positions. The dominant morphotypes comprising the grass phytolith percentage were rondel short cells and several types of elongate cells observed only in grasses in the reference collection. Extremely few bilobate phytoliths (<0.1% on all plots) were found, indicating none of the bilobate-producing grasses, *A. lemmonii*, *D. unispicata*, and *M. aristata*, had significant prehistoric cover on any of the plots. All ridge-top plots had >10% *P. ponderosa* spiny bodies and spiny rods throughout the soil profile, indicating long-term presence of this species there. All plots contained substantial percentages of non-diagnostic phytoliths, dominated by several non-diagnostic types of elongate cells, but also including blocky polyhedrals, tracheary elements, epidermal cells, mesophyll cells, and hair cells (Piperno 2006). Although non-diagnostic phytoliths were counted, they were not quantitatively categorized because the reference material suggested these types would not provide useful information due to considerable redundancy between species. However, there were few obvious differences in the assemblage composition of non-diagnostic phytoliths in relation to soil depth or between plots. Many of these non-diagnostic morphotypes may have been produced by grasses.

DISCUSSION

The lack of diagnostic phytoliths in most of the reference material was in agreement with other studies of similar species. The only surprising result was the *Pseudotsuga menziesii* (Mirbel) Franco var. menziesii (Douglas-fir) sample contained no diagnostic asterosclereid phytoliths observed by several others (Brydon et al. 1963; Norgren 1973; Blinnikov 2005). One explanation (although there is no supporting mineralogical data available) is that if the soils on the site are rich in aluminum and/or iron oxides, silica in solution available to plants for phytolith formation may be reduced considerably (Beckwith and Reeve 1963; Jones and Handreck 1965). Other plausible explanations are the needles collected were too young to have much silicification or the asterosclereids may have been present but damaged in processing, broken into pieces that were unrecognizable.

Grassland soils have been found by various researchers to contain at least 5–10 times more phytoliths by weight than forest soils, which generally have phytolith content between 0.1 and 0.5% by weight (Table 3). A site in the *P. ponderosa*-bunchgrass vegetation type in northern Arizona (7–50% grass cover in the understory), probably the closest phytolith analog for Sierra Nevada mixed conifer forests if they had a prehistoric grass understory, showed total phytolith content of 1–1.4% (Kerns 1999; Kerns et al. 2001). Grass phytoliths made up approximately half of the total, *P. ponderosa* the other half (B. Kerns personal communication).

Phytolith concentration on hillside plots in our study was at the low end of published data, even for forest plots. The paucity of phytoliths observed in most plant reference material species (Table 1) suggests that very few phytoliths would be deposited in the soil unless substantial cover of heavy phytolith producing plants not present on the plots today (*P. ponderosa*, grasses, or sedges) were present on the plot for a substantial period of time in the past.

Ridge-top plots had phytolith concentrations within the expected range for forest soils, but considerably less than found at the *P. ponderosa*-

bunchgrass site in northern Arizona. *Pinus ponderosa* and bunchgrasses are currently minor components of the vegetation on these plots; grasses (mostly *Bromus carinatus* Hook. & Arn. and *Elymus elymoides* (Raf.) Swezey) are present with <5% cover. The phytolith evidence suggests that *P. ponderosa* and bunchgrasses were prehistorically present but have remained minor components of ridge-top vegetation.

Lower channel-side plots had higher grass phytolith concentration than expected for forest soils, but less than half the concentration typical of grassland. There are currently very few grasses in this part of the watershed. One possible explanation is that there was a prehistoric stringer meadow associated with the stream that disappeared when the water table dropped due to down-cutting. This interpretation is supported by data from phytolith sampling of a small stringer meadow in the mixed-conifer forest in the Sierra San Pedro Martir in Baja California, that had total phytolith weight and percentage of grass phytoliths comparable to these plots (R. Evett et al. In Press).

Phytolith migration and dissolution, alternative explanations for low soil phytolith weights, must be ruled out before the grass understory hypothesis can be rejected. Because they are mostly silt-sized particles, phytoliths are known to migrate downward in the soil profile, particularly in sandy soils (Starna and Kane 1983). Sampling at several depths in soil pits revealed no evidence of substantially fewer phytoliths at the surface or accumulation of phytoliths at any depth (Table 2). Phytolith degradation and dissolution is known to occur under alkaline soil conditions but only under the most severe acidic conditions (Piperno 2006). The soil type sampled, the McCarthy series, is slightly acidic (pH 6.3–6.4) (Walfoort and Hunt 1982), which provides ideal conditions for soil phytolith preservation. Phytolith migration and dissolution are not plausible explanations for the lack of grass phytoliths in South Grove soils.

In the absence of phytolith migration, it is reasonable to expect increasing phytolith age and decreasing phytolith concentration with increasing soil depth (Alexandre et al. 1999; Piperno 2006). Although no dating was attempted (and would be difficult to interpret because of bioturbation issues), phytoliths from each sampled soil profile probably span at least the past 1500 yr, the age of the oldest living *S. giganteum* in the stand, but more likely several thousand years.

The phytolith evidence indicates that grasses, while certainly present, have not been a major component of the *S. giganteum* forest understory in the South Grove Natural Preserve. We conclude that grass was not likely to have been present with enough cover to be a major source of fine fuel required to carry frequent prehistoric ground fires in this *S. giganteum* stand. Because none of the other plant species examined (except for sedges and *P. ponderosa*) produced diagnostic phytoliths, the prehistoric presence of deciduous trees, shrubs, or other herbaceous species in the understory could not be determined from phytolith evidence. There is the possibility that more detailed work, beyond the scope of this study, analyzing many more samples of reference material from other sites, could identify more diagnostic phytoliths and signature phytolith assemblages to shed more light on the presence of prehistoric understory species.

Other research supports the conclusion that grass was not a substantial component of the giant sequoia forest understory. For example, even under the high levels of light that exist after logging, Biswell et al. (1966*a*) found that grass-like plants had less than 10% frequency in giant sequoia forests. Phytolith data from a relatively open, mixed conifer forest in the Sierra San Pedro Martir, Mexico, suggest that grasses may not have been a major component of the understory (R. Evett et al. In Press).

Parsons (1978) found at Redwood Mountain (approximately 100 km south of Calaveras Big Trees State Park and 550 m higher elevation) that forest floor fuel loads following the first prescribed fire in a *S. giganteum* stand were similar to unburned stands 7 yr following burning; however, he attributed much of this fuel to material killed by the prescribed fire from *A. concolor* that had invaded the giant sequoia stands during the past 100 yr when fire was absent. Parsons predicted that a second prescribed fire would remove this fuel source; it was unclear where additional fuel to support a short fire interval would come from. This is in contrast to data from (Biswell 1966*b*), who found that *S. giganteum* stands produced large amounts of litter each year, ~9000 lbs/acre.

It is possible that deciduous hardwoods co-occurring with *S. giganteum* provided sufficient surface fuels prior to the mid-1800's to achieve an average five year fire interval. As a result of livestock grazing and the altered fire situation for the past 150 yr, hardwoods such as *Quercus kelloggii* (black oak) are now uncommon in *S. giganteum* stands (Biswell et al. 1966*a*; Bonnicksen and Stone 1982). Further research is necessary to investigate the possibility of hardwoods as a fuel source.

Parsons (1995) stated that fire in giant sequoia stands stimulated shrub and hardwood growth. The patchy nature of natural fires, with irregular shapes and varying rate of spread, and role of occasional intense fires (Stephenson et al. 1991) provides opportunity for shrubs to provide a significant amount of fuel. Common shrubs in the vicinity of giant sequoia stands include

Chamaebatia foliolosa Benth. (mountain misery), *Ceanothus cuneatus* (Hook.) Nutt. (buckbrush), *Ceanothus integerrimus* Hook. & Arn. (deerbrush), and *Chrysolepis sempervirens* (Kellogg) Hjelmq. (bush chinquapin). Of these, *C. foliolosa* seldom occurs in *S. giganteum* stands and would be displaced by frequent burning. *Ceanothus* species are known to invade areas following disturbance but have never been commonly found within *S. giganteum* stands. *C. sempervirens* burns well but is typically only dense on north-facing slopes. Because phytolith analysis provides no information on these shrubs, resolving the question of their abundance in *S. giganteum* stands remains problematic. *Ceanothus cordulatus* Kellogg and *Chamaebatia foliolosa*, although lacking in diagnostic phytoliths, produce enough biogenic silica (Table 1) to contribute considerable quantities of phytoliths to the soil. Further study of their phytolith assemblages in reference material may eventually produce a soil phytolith assemblage signature for these two shrubs.

There also are several alternative explanations, not requiring post-European settlement changes in the forest understory, which could account for the lack of success achieving fire return intervals approaching five years with prescribed burning at the South Grove Natural Preserve. The simplest explanation is the five year estimate is based on a composite of 2000 yr of tree-ring fire-scar data from five *S. giganteum* groves along a 160 km transect in the Sierra Nevada, with substantial variation between groves and substantial variation at decadal and centennial scales correlated with fluctuating climate (Swetnam 1993). The South Grove Natural Preserve is further north than any of the sampled groves and may be more mesic, while the current climate of the region may also be more mesic than average (Cook et al. 2004, Grid 47), leading to a longer than average expected fire return interval. Also, if very small fires (recorded by only a single tree) are excluded, the mean fire return interval for three of the five *S. giganteum* groves sampled is close to 10 yr (Swetnam et al. 1992).

Miller and Urban (1999), based on a model of the surface fire regime in mid-elevation coniferous forests of the Sierra Nevada, suggested the fire return interval depends on forest floor fuel load and fuel moisture. Their model indicated that even without a grass understory, there may be sufficient fuel accumulation on the forest floor to support a five year or less fire return interval under conditions of very low (<5%) fuel moisture (Miller and Urban 2000). Their simulations showed that under average climate conditions, with no grasses or shrubs in the understory, the mean fire return interval at the elevation of the South Grove Natural Preserve should be ~6 yr (Miller and Urban 1999). According to the model, a five year accumulation of *S. giganteum* litter should be enough to carry at least a patchy fire, but perhaps only under more extreme weather conditions (low humidity, high temperature, high wind) that are not always accompanied by an ignition source. Many of the fires seen in the tree-ring fire-scar record may have been intentionally set by humans whenever extreme conditions were present, without concern for catastrophic fires because they knew the intensity would be very low. Because of safety concerns, prescribed burning typically occurs during periods with higher levels of fuel moisture when effective fuel connectivity is much lower. Because considerably more fuel accumulation is required to carry an extensive prescribed fire, a longer fire return interval would be expected.

Given the short prehistoric fire return interval and more widely spaced trees, litter build-up was probably very uneven on the forest floor, leading to highly patchy, low intensity fires. This has been observed in mixed conifer forests in the Sierra San Pedro Martir, where forest structure remains relatively open because of a continuing fire regime (Stephens et al. 2003). The mean fire return interval, based on the frequency of occurrence of all fires on a sampled site, may be misleading if there are frequent, small fires that burn very little area; burning every part of the stand may take considerably longer. A 25% composite mean fire return interval, calculated from fires scarring >25% of the recording trees in a stand, may be more useful to estimate the frequency of widespread fires in a highly patchy environment (Dieterich 1980; Swetnam and Baisan 2003). Another better measure in this patchy situation may be the fire rotation period, defined as the average length of time between fires averaged for each fire-scar recording tree (Baker and Ehle 2001). This gives an estimate of the maximum time required to burn an area the size of the stand, and may more accurately represent temporal burning patterns in *S. giganteum* stands. Expecting a prescribed fire to burn through an entire stand every five years is probably unrealistic. Mean fire return intervals estimated using the 25% filter or fire rotation period would be considerably longer than five years and probably more indicative of the time required to burn the entire stand. The currently observed 15–20 yr period required for enough fuel to accumulate between prescribed fires given the present climate may be representative of the fire regime under a similar climate in the past.

The management goal for Calaveras Big Trees State Park is to ensure natural processes are the principal influence on *S. giganteum* stands so that large, exceptional specimens can grow to maturity and the species can regenerate naturally. Current forest conditions, because of past logging

and fire suppression, have created an environment wherein *S. giganteum* does not regenerate naturally because of a lack of surface fire, and large mature trees are at risk from catastrophic crown fires carried by the tightly crowded thickets of fir and pine trees that have developed in the absence of surface fires. Through phytolith analysis, an inexpensive approach to definitively test for the presence of prehistoric grass, we have shown that the prehistoric frequent fire regime at South Grove Natural Preserve probably did not depend on a grass understory. Grass should probably not be a major part of management strategies seeking to mimic prehistoric fire regimes. The South Grove is typical of other stands of *S. giganteum* in the central Sierra Nevada. The results of this study, if replicated at other locations, may be applicable to *S. giganteum* fire management in a much wider region.

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THE ROLE OF FIRE REFUGIA IN THE DISTRIBUTION OF *PINUS SABINIANA* (PINACEAE) IN THE SOUTHERN SIERRA NEVADA

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ABSTRACT

Although widespread throughout the interior foothills of central and northern California, *Pinus sabiniana* Dougl. has a disjunct distribution in the southern Sierra Nevada, where it is abundant in the Kern River and Tule River watersheds, but is absent from the Kaweah River watershed between 36° and 37°N. This gap in the pine's distribution has long intrigued botanists and ecologists and has elicited a number of hypotheses for this anomalous biogeographical pattern. Here we propose a new hypothesis that couples unique features of the southern Sierra Nevada topography with unique features of *P. sabiniana*'s response to fire. This low elevation pine is widely distributed in grassland and chaparral, and where it occurs with the latter vegetation, it is extremely vulnerable to high intensity wildfires. Under these conditions, meta-populations persist over time in refugia in riparian areas and during fire-free intervals expand outwards re-colonizing shrubland dominated slopes. The lack of such refugia in the very steep and narrow Kaweah drainage is hypothesized to explain the absence of this pine in that area. To test this hypothesis, we studied the age-structure of *P. sabiniana* in the area of the 2002 McNally Fire in the Kern drainage to compare age distributions of trees and tree skeletons along a gradient up slope away from riparian zones. Maximum age declined significantly with distance from riparian areas, suggesting that past fires have eliminated *P. sabiniana* from the slopes and that the pines have re-colonized during fire-free intervals. The relationship was strongest when our data were restricted to areas that had a previously recorded fire. We also found that the riparian areas in the Kern drainage were significantly wider than those in Kaweah drainage, suggesting that fewer such fire refugia exist in the latter watershed, and providing an explanation for the lack of *P. sabiniana* between 36° and 37°.

Key Words: chaparral, digger pine, fire severity, foothill pine, gray pine, Kaweah, Kern, meta-populations.

The California endemic *Pinus sabiniana* Dougl. (Pinaceae) is a conspicuous tree in the semi-arid foothills of the ranges ringing California's Great Central Valley. This species often occurs in open stands in association with chaparral and woodlands between 150 and 1200 m elevation (Sudworth 1908), with a lower elevation limit somewhat higher (300 m) in the southern portion of its range.

A strange feature of *P. sabiniana*'s distribution is a 90 km north-south gap in the southern Sierra Nevada foothills (Fig. 1). For no easily explainable reason, *P. sabiniana* is absent between the Kings River, Fresno County and the South Fork of the Tule River, Tulare County despite the existence of seemingly suitable habitat. This peculiar gap was commented on by Josiah D. Whitney in 1865 (cited in Griffin and Critchfield 1972) and has been noted by many other authors (e.g., Jepson 1910; Graves 1932; Ledig 1999; Brake 2005). Ledig (1999) has argued that this gap in *P. sabiniana's* range results from late Pleistocene–early Holocene lakes blocking the pine's dispersal as it migrated into the Great Valley from the Transverse Ranges of southern California. This model depends upon the Pleistocene Tulare Lake being a sufficient barrier to prevent dispersal across the lake and leaves unexplained why there was a lack of northward migration in the foothills between the Kaweah and Tule drainages. Although *P. sabiniana* has a relatively limited mean dispersal distance (Johnson et al. 2003), which might be important on short time scales, rare dispersal events (such as seed dispersal by jays) might be expected to overcome these barriers on longer time scales, as has been documented for some pines (Vander Wall and Balda 1977). Recently, Brake (2005) proposed an alternative explanation for this distribution gap, which was that increased species diversity in the area of the gap has competitively excluded *P. sabiniana* from this region.

Graves (1932) proposed that this distribution gap between the Kings and the S. Fork of the Tule rivers could be explained on the basis of fire. His hypothesis was that some large historical fire or fires had extirpated *P. sabiniana*, but it did not explain why the gap should be in this particular region. Also addressing this range discontinuity, Watts (1959) suggested that Native American burning in the Kaweah may have resulted in large fires that excluded *P. sabiniana*.

Fire is an important part of *P. sabiniana's* ecosystem as well as for the majority of pine

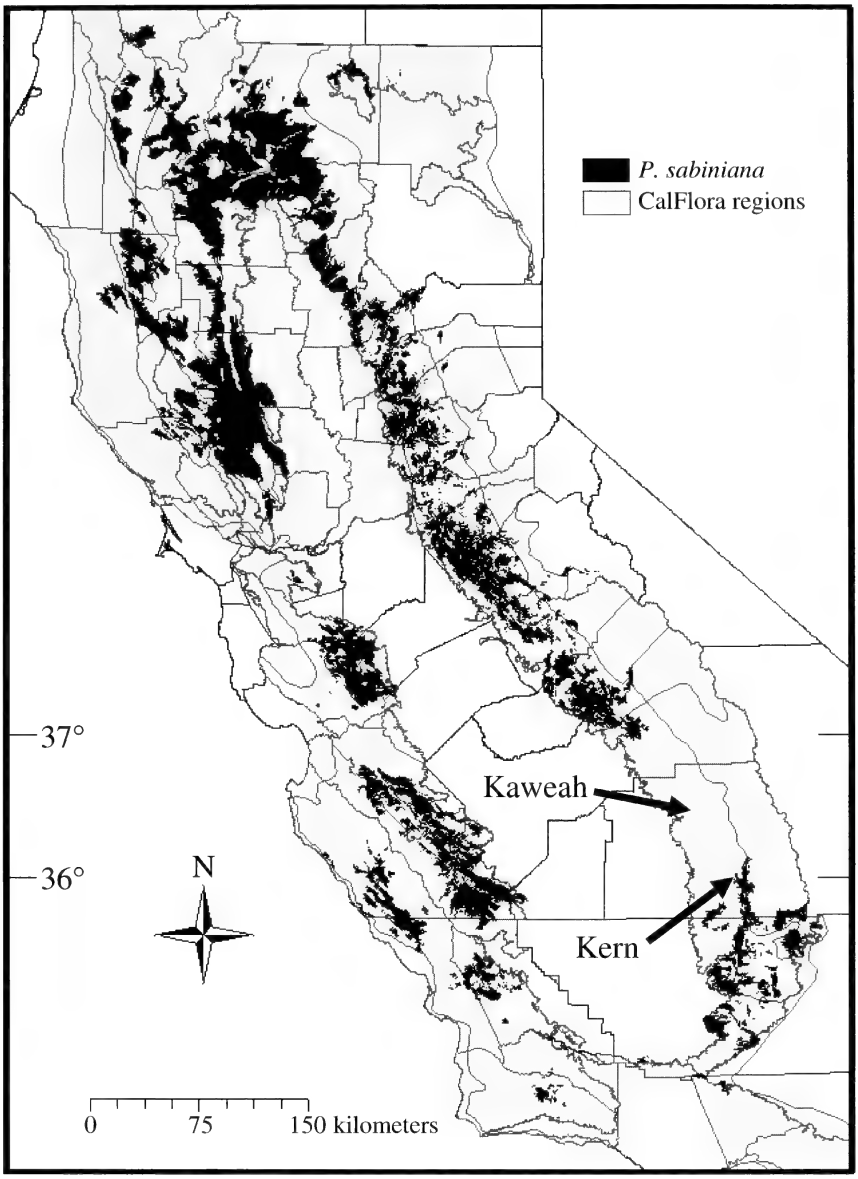

FIG. 1. *Pinus sabiniana* distribution (shown in black) in California according to the GAP Analysis Project (USGS 2006). The Jepson/CalFlora regions where *P. sabiniana* may be expected to occur are shown in gray (Hickman 1993), however, this pine is absent from the Southern Sierra Nevada between 36° and 37°N, which includes the Kaweah watershed indicated on the map. Also, indicated is the Kern drainage where the field study was conducted. Other areas mentioned in the text include the Kings River to the north of the Kaweah and the Tule River west of the Kern.

species. Pines in fire-prone regions fall generally into one of two groups: those in surface-fire regimes that survive fire through thick bark, greater mature height, and self-pruning of dead branches, and those in crown-fire regimes that have more flammable architectures and are easily killed by fire, but have serotinous cones that cue seedling establishment to take advantage of extensive fire-cleared gaps (Keeley and Zedler 1998). Schwilk and Ackerly (2001) have placed these strategies into an evolutionary context and argued that they have resulted from a repeated pattern of correlated evolution between the "fire-surviving" and the "fire-embracing" strategies that comprise suites of structural and life-history traits. Although these patterns appear to hold up for most pines, and over widely separate parts of North America, three low elevation California pines, *P. sabiniana*, *P. coulteri* D. Don, and *P. torreyana* Carrière, appear somewhat anomalous (Keeley and Zedler 1998). *Pinus sabiniana* has traits such as thick

bark (Johnson et al. 2003) similar to the "fire surviving" pines, but does not self-prune dead branches and does not typically survive fire (Graves 1932; Lawrence 1966; Borchert et al. 2002). Furthermore, *P. sabiniana* has cones that are generally not serotinous, although (Johnson et al. 2003) have argued that seeds cached in the soil by animals provide an alternative local dispersal mechanism in place of serotiny for *P. sabiniana* and its close relatives *P. coulteri* and *P. torreyana*.

Largely unexplored to date is the possibility that there are unique attributes of the Kaweah watershed that may explain the gap in *P. sabiniana* distribution. This is a region of anomalous topography: The transition from the Great Valley to the Sierra Nevada is steeper and more abrupt here than it is north or south of this area. Saleeby and Foster (2004) argue that the area between 36° and 37°N (which corresponds nearly exactly to the gap in the *P. sabiniana* distribution) represents a region of convective mantle "drip" centered west of the Sierra Nevada: subsidence results in the steeply faceted mountainous topography here actively being buried under the sediments of the Great Valley. Comparing sites within the gap to sites north and south of the gap, Brake (2005) found that the sites in the distribution gap had increased slope and more exposed rock.

While we doubt that steep terrain alone can explain the lack of *P. sabiniana* in this region, we believe that when coupled with the following observations on fire response, it may indeed contribute to the absence of this pine in the Kaweah drainage. South of the Kaweah watershed there are extensive stands along the Kern River and its tributaries north of Kernville. Much of the middle and lower Kern watershed burned in the McNally Fire during July, 2002. Because this low elevation pine is commonly interspersed in chaparral shrublands, fires are typically large and of high intensity. After the fire, we observed that many thousands of pines were killed and pines survived primarily in the broad alluvial areas that parallel watercourses (Fig. 2). Most trees outside of these river valleys were killed and very little seedling recruitment was observed in the area of the McNally burn (Keeley et al. 2005).

In light of these observations, we propose a new model for pines in fire prone habitats that differs from the fire embracing and fire surviving models of pine-fire coexistence. This is the fire refugia model and it is offered as an explanation for both the long term persistence of *P. sabiniana* in landscapes such as the Kern that are periodically subjected to high intensity crown fires and explains the biogeographical gap in its distribution centered on the Kaweah watershed. We hypothesize that periodic high intensity fires eliminate *P. sabiniana* from many upland sites and that meta-populations survive such events by persistence in refugia in the bottoms of ravines and alluvial plains. During the intervals between fires pines re-colonize slopes and persist until the next high intensity fire. Thus, we imagine the population dynamics of this pine to be one of periodic fire-induced contraction and expansion. This hypothesis is similar to the model proposed by (Zedler 1981) for closed-cone cypress, and to that suggested by (Keeley 2006) for big-cone Douglas fir in the Transverse Ranges of southern California. We suggest that the distribution gap in the Kaweah watershed results from it being a region of steeper topography that lacks broad, riparian refugia.

The purpose of the present study was to test this fire refugia hypothesis by investigating patterns of pine distribution in the 2002 McNally Fire. We predicted that if *P. sabiniana* must re-colonize hillsides from refugia, then we should see a shift in pine age structure along a gradient from the valley bottoms up the slopes, with tree age declining along the gradient. In addition, we investigated our biogeographical gap hypothesis by testing the prediction that the width of potential riparian refugia would be smaller in the Kaweah drainage than in the Kern.

Methods

The McNally Fire burned 25,100 ha of the lower Kern watershed of Sequoia National Forest during July 2002. We randomly selected seven transects within the area burned by the McNally Fire, with the requirement that each of the four accessible main drainages within the burn that contained *P. sabiniana* habitat were represented by at least one transect. These drainages were the Kern below the confluence with Brush Creek, Brush Creek, South Creek, and the North Fork of the Kern above the confluence with South Creek. Transects were positioned by selecting a random point along the bottom of the drainage within a pre-selected section several km long and placing the transect directly parallel with the fall line at that point. Transects were 50 m wide and 500 m long. Transects began at the watercourse in the valley bottom and proceeded directly perpendicular to the lower slope contour. This resulted in transects that generally increased in altitude, but occasionally crested side ridge lines and descended slightly near the end.

Within each transect, every *P. sabiniana* individual (alive or dead) was recorded and its position marked with a GPS unit. The diameter at 50 cm height was measured on each tree. To determine a diameter-age relationship, we cut slabs for counting rings from 29 trees over a wide a range of diameters. For aging, we attempted to distribute our sampling over a range of eleva-

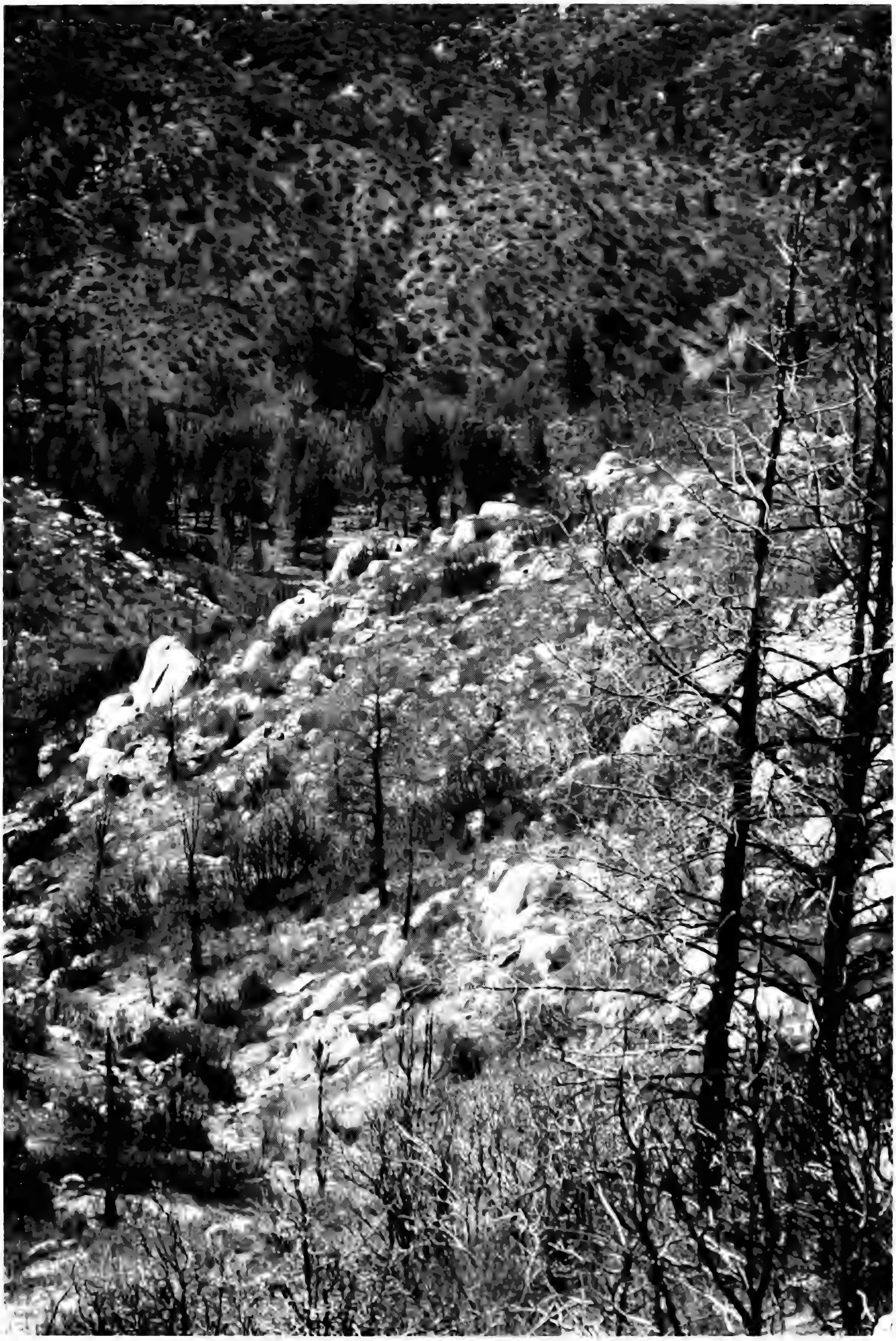

FIG. 2. Example of a *P. sabiniana* stand in an alluvial corridor that survived the 2002 McNally Fire in the Kern watershed, whereas all pines on the slopes above were killed.

tions, but for larger trees that would be dangerous to fell, we were limited to trees already felled after the fire by the USDA Forest Service as hazard snags along the roads and near campgrounds. We aged trees that fell outside the transects as well as those inside to increase

our sample range. It was possible to cross-date approximately one third of the trees by matching narrow rings with known drought years in this region (drought years supplied by Tony Caprio, NPS, Sequoia-Kings Canyon).

Our hypothesis predicts that maximum tree age should decrease with distance from the putative refugia in the riparian zone. In other words, we should expect young and old trees low in the transect, but only young trees high in the transect. To test this, we used quantile regression on age versus distance. We wish to test how the maximum tree age changes with distance and quantile regression is useful for cases such as this where we are interested in how the extreme changes, rather than the mean (Koenker and Bassett 1978). We explored quantiles (τ) of 0.85, 0.90 and 0.95. All statistical analyses were conducted with the R statistical language (R Development Core Team 2005). The R quantreg module was used for quantile regression. Using fire-history data maintained by the U.S. Forest Service since 1910, we categorized our transects into two groups: those that had experienced a previous fire and those that had no recorded fire history prior to the 2002 burn. One transect had burned in 1934 and two had burned in the same fire in 1940. In the areas with no previously recorded fires, we cut stem sections from standing skeletons of non sprouting *Arctostaphylos viscida* C. Parry. Although the center of the stems were often rotted, we counted 107–127 rings in individuals at two locations and estimated ages of between 130 and 150 yr (unpublished data, Keeley et al. 2005).

To test our hypothesis that the Kaweah watershed may provide fewer fire refugia than the Kern, we compared the topography of the two watersheds. We characterized the distribution of slopes within each watershed between 300 and 1800 m using a geographic information system (ARCGIS, ESRI) and USGS digital elevation data to test for a difference in overall steepness, which may influence fire intensity. To test for differences in the distribution of potential riparian/alluvial refugia, we measured the average width of riparian areas in six stream/river drainages in each watershed, with two to three measurements at random points along each stream. We defined this width as the distance between opposite slopes containing a stream drainage in which the slope was less than 30 degrees. The drainages were selected at random among a set of 10–15 potential drainages per watershed. These widths were calculated using the USGS 7.5 min maps.

RESULTS

We counted rings on 29 trees to develop a diameter-age prediction equation. The approximate ages ranged from 9 to 112 yr (8–113.5 cm). A linear regression described the relationship between basal diameter and age ($F_{1,26} = 121.9$, $P < 0.001$, $r^2 = 0.82$). We predicted age for all trees according to the resulting equation: age = 0.7766 × diameter + 14.28. Predicted ages ranged from 14 to 101 yr (Fig. 3). We divided our aged trees into two samples, slope and valley stream bottom to test for a different diameter-age relationship depending upon location, but found no evidence for such a difference. We therefore used the overall regression to predict ages.

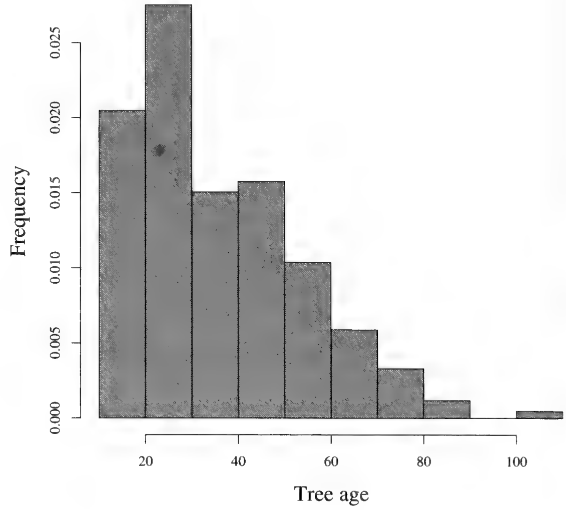

FIG. 3. Predicted age distribution for all *P. sabiniana* using pooled data for seven transects (N = 425), where age = 0.7766 × basal diameter + 14.28.

Transects began in the level riparian/alluvial areas and left the stream alluvial area within 10–50 m. The hill slopes themselves varied from 15–30° in steepness. Quantile regression on predicted age as a function of distance from the base of the transect resulted in negative regression slopes for each of the 7 transects. A single sample t-test on these slope values indicated that the mean slope (−0.05) was significantly different from zero ($t = -3.94$ $df = 6$, $P = 0.007$). Figs. 4 and 5 show the age/distance results for all seven transects.

Using fire-history information maintained by the U.S. Forest Service, we categorized transects into those that had experienced a fire previous to the 2002 burn (Fig. 4) and those that had no recorded fire (Fig. 5). The mean quantile regression slope for transects in areas that had burned previously was significantly lower (more negative) than the mean slope for areas that had not experienced a previous fire (means = −0.073 and −0.018, Kruskal-Wallis $\chi^2 = 4.5$, $P = 0.034$). These results were consistent across several values of τ (Table 1).

Although all transects had burned in the 2002 McNally Fire, some trees survived even this very intense fire. Logistic regression on the probability

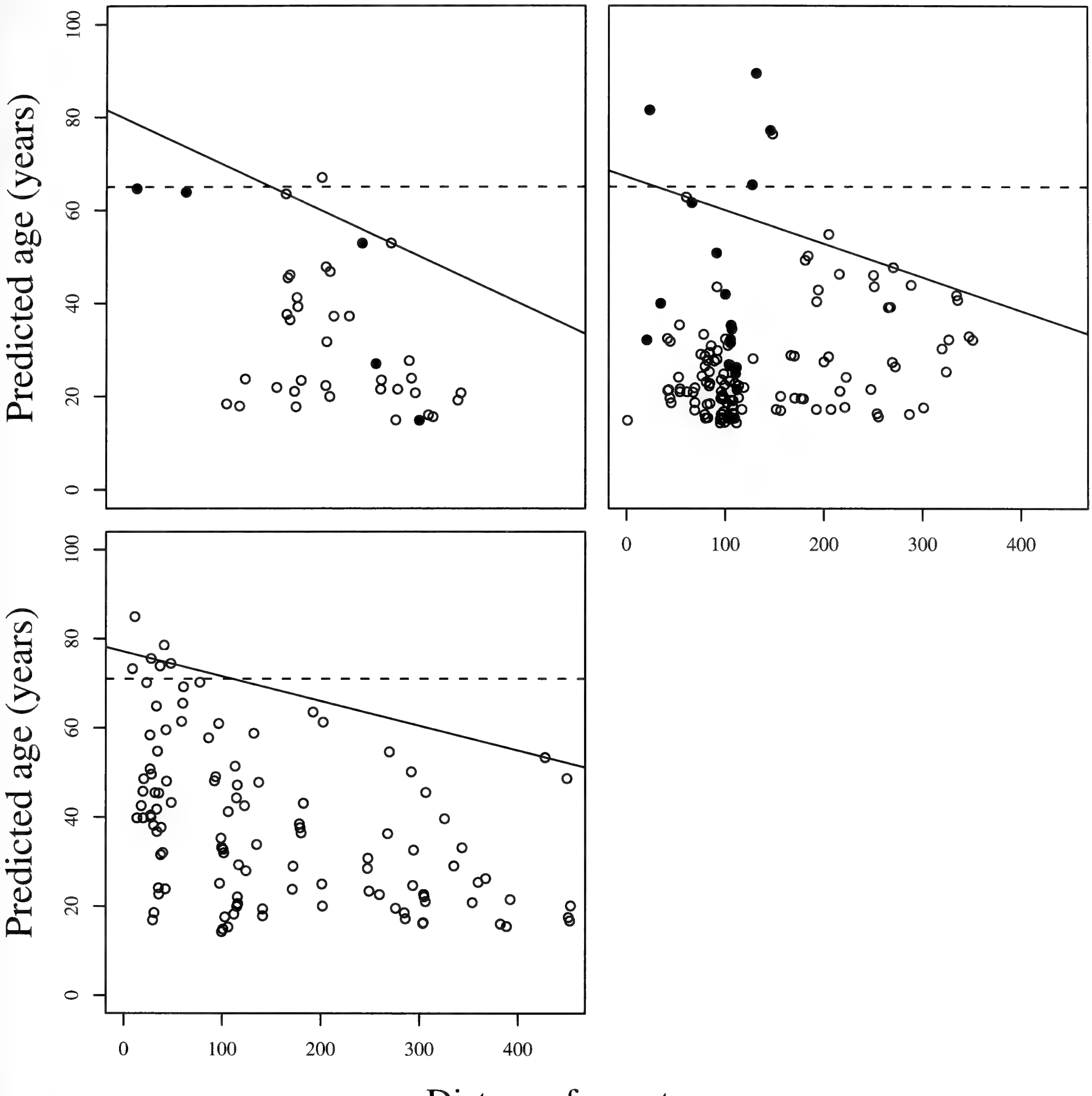

FIG. 4. Age vs distance relationship for the three transects that occurred within the boundaries of a recorded fire prior to the 2002 McNally Fire. Solid circles show trees that were alive following the McNally fire; open circles show dead trees. Solid lines show the $\tau = 0.95$ quantile regression. The mean quantile regression slope was -0.018. The dashed lines indicate the time of the last recorded fire prior to the McNally burn.

of tree mortality reveals that distance from the valley bottom significantly increased mortality (model: likelihood of survival = distance + transect, Wald $Z = -4.22$, $P < 0.001$). The mean distance for living trees was 126.1 m and the mean distance for dead trees was 170.3 m.

Mean slopes within *P. sabiniana's* elevational range did not differ significantly between the Kern and Kaweah watersheds nor did the proportion of very flat terrain (slope $< 5°$): the proportion was approximately 6% for both watersheds. This measurement does not distinguish between valleys and plateaus, so we also investigated valley widths, which may better correspond to fire refugia. However, the average width of riparian/alluvial valleys did differ significantly between the two watersheds. The average width in the Kern was 177 m ($\tau = 138$) and in the Kaweah it was 79 m ($\tau = 41$) (t-test, $N = 32$, $p = 0.013$).

DISCUSSION

Our study supports the hypothesis that *P. sabiniana* in the Kern watershed must re-invade the slopes after being eliminated by severe

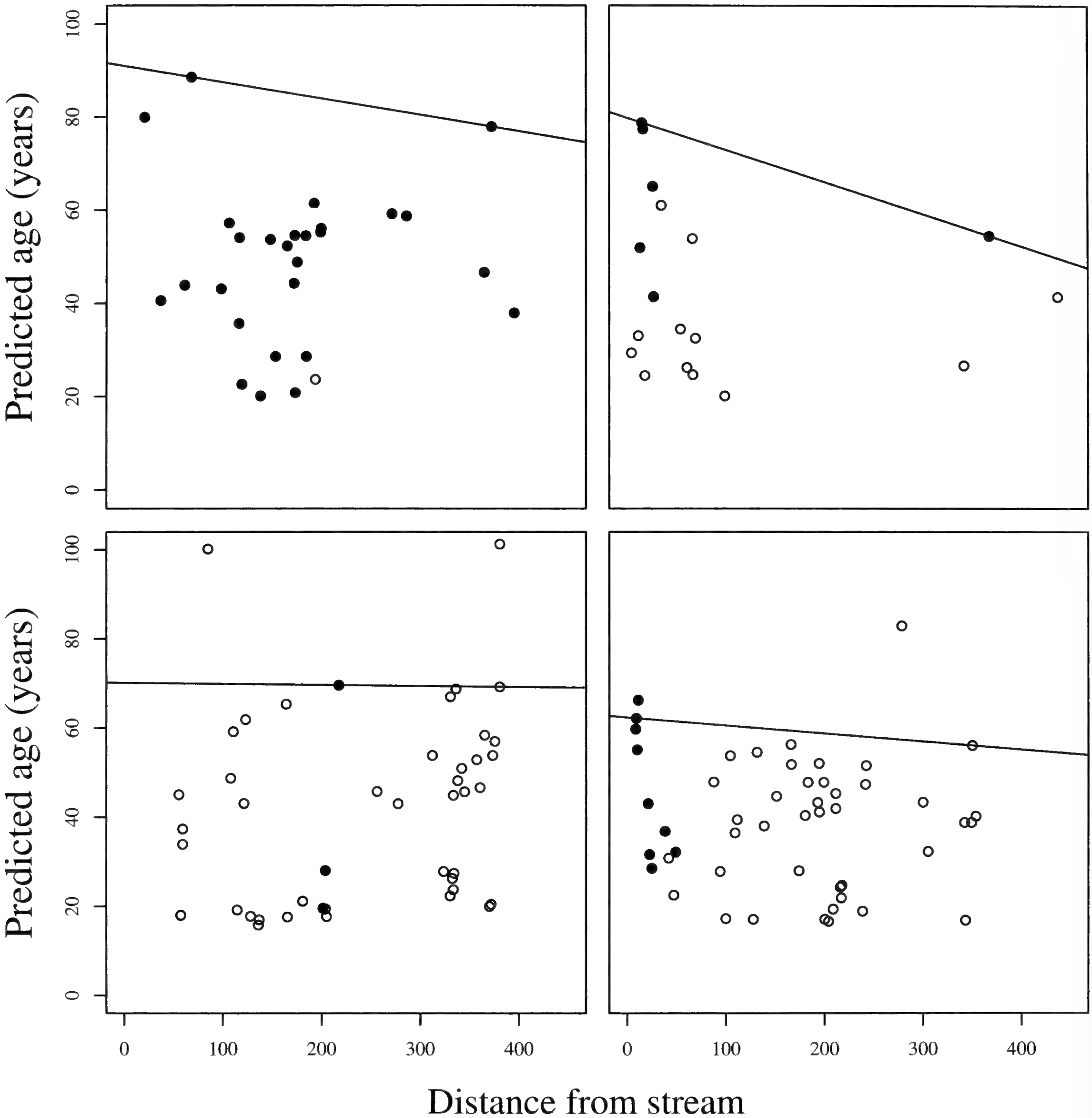

FIG. 5. Age vs distance relationship for the four transects that had no recorded fire prior to the 2002 McNally Fire. Solid circles show trees that were alive following the McNally Fire and open circles show dead trees. Lines show the τ=0.95 quantile regression. The mean quantile regression slope was −0.073.

wildfire. The decrease in upper quantile tree age with distance from the stream or valley bottom is consistent with the hypothesis that this re-colonization from valley bottom fire refugia is a gradual process. Many chaparral plants that are killed by fire have a soil-stored seed-bank and fire-cued germination that allows for rapid population recovery following fire. In contrast,

TABLE 1. QUANTILE REGRESSION SLOPE ESTIMATES AND 0.95 CONFIDENCE INTERVALS ON SLOPES FOR THREE VALUES OF τ. Data from all transects were pooled into the two categories according to past fire history prior to the McNally Fire.

	τ = 0.85			τ = 0.90			τ = 0.95		
	slope	conf. bounds.		slope	conf. bounds		slope	conf. bounds	
Recorded fire	−0.056	−0.101	−0.014	−0.059	−0.093	−0.033	−0.058	−0.090	−0.043
No recorded fire	−0.009	−0.029	0.035	0.001	−0.052	0.022	−0.026	−0.033	0.033

recovery by *P. sabiniana* appears to be much slower. We estimated ages of non-sprouting *Arctostaphylos viscida* at 130–150 yr those sites with no previous recorded fire. *P. sabiniana* individuals near these *Arctostaphylos* were much younger (20–30 yr), indicating that the pines had recruited years after the last fire prior to the McNally Fire. In fact, the maximum age of *P. sabiniana* sampled in this study was approximately 100 yr (Fig. 3). Thus, it is apparent that in a chaparral dominated landscape, which experiences recurring intense fires, this tree is dependent upon fire refugia for long term persistence. As a result, this pine exhibits population fluctuations quite unlike those of other pine strategies. For example, the fire-surviving strategy of ponderosa pine results in only small localized gaps that are rapidly re-populated from parent trees surrounding the gaps. The fire-embracing strategy of knobcone pine results in total population annihilation but regeneration in situ from a serotinous seed bank. This third model of pine life history depends on meta-populations, whereby populations shrink and persist in refugia, but expand outwards during fire-free intervals.

Short-range dispersal in *P. sabiniana* may act to maintain the age-distribution gradient. *P. sabiniana* seeds have an extremely reduced wing and are not dispersed easily by wind, but appear dependent upon animal seed dispersal (Keeley and Zedler 1998; Johnson et al. 2003). Investigation of the closely related *P. coulteri* has shown that seeds are dispersed by scatter-hoarding rodents close to the parent tree with a mean distance of 15.3 m (Borchert et al. 2003). *P. sabiniana* reaches maturity at 10–20 yr (Krugman and Jenkinson 1974), although seeds on trees as young as two years have been recorded (Watts 1959). Limited dispersal and a moderate age to reproduction seem to combine to slow the advance of this tree into burned areas.

Since our data from the Kern watershed shows that *P. sabiniana* depends upon fire-protected refugia, a lack of such refugia in the region of the distribution gap may explain the discontinuity in the species's range. The difference in mean valley widths between the Kern and the Kaweah watersheds does indicate that the Kern may provide better fire refugia than does the Kaweah, and therefore a higher probability of long-term population persistence. In addition, although our comparison of mean slopes according to digital elevation models did not detect a statistically significant difference in average steepness between the Kaweah and the Kern, previous work by (Brake 2005), did find significantly steeper slopes in the gap than at similar elevation sites to the north and south.

However, riparian areas and alluvial plains are not the only potential fire refugia for pines. Rocky outcrops on slopes allowed some pines in the Kern to survive the McNally Fire and there are some rock outcrops in the Kaweah drainage. Although we have not investigated this closely, it appears from our observations that the combination of steep terrain and dense vegetation of the Kaweah may readily carry fire into such rock outcrops, thus diminishing their value as refugia. Although fire refugia appear to be important to *P. sabiniana* in the southern Sierra Nevada, this pattern of stand-replacing fires restricting populations to refugia may not apply across *P. sabiniana's* entire range. In areas were the pine grows within a matrix of grassland, it may not be subject to the same stand-replacing fires it experiences in the Kern where it grows among chaparral. Knowledge of the fire-response and age structure throughout *P. sabiniana's* range, as well as the degree of variation in cone and bark traits within the species, would help us better understand the life history and biogeography of this pine.

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FIRE SEVERITY AND PLANT AGE IN POSTFIRE RESPROUTING OF WOODY PLANTS IN SAGE SCRUB AND CHAPARRAL

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ABSTRACT

Postfire resprouting by woody plants confers a marked advantage in rate of recovery over species that regenerate entirely from seed. However, the predictability of this advantage varies markedly between species, with some showing nearly 100% rootcrown survival and others often much lower. This study examined patterns of fire-caused mortality and tested the relative importance of fire severity and plant age between various shrubs and subshrubs characteristic of chaparral and sage scrub associations. Resprouting success varied from about 10% for *Eriogonum fasciculatum* to a high of 98% for *Quercus berberidifolia*. For most of the shrub species, skeletons of resprouting plants were significantly taller than those of dead individuals of the same species, indicating less biomass consumption, and thus lower severity fires were associated with higher resprouting success. This pattern was less strongly the case with sage scrub species. Shrubs and subshrubs, however, differed in the effect of aboveground plant age (as estimated by basal diameter) on resprouting success. For most chaparral shrubs, age was not related to resprouting success, whereas in four out of five subshrub species, including *Artemisia californica*, *Eriogonum fasciculatum*, *Salvia leucophylla*, and *S. mellifera*, the youngest plants exhibited the highest resprouting success. I hypothesize that the reason for this inverse relationship between age and resprouting in certain sage scrub species is that, as these subshrubs age, there is a tendency to loose the resprouting ability and the mechanism is quite possibly because adventitious buds responsible for sprouting become buried by woody tissues. Patterns of character evolution in these sage scrub lineages support the hypothesis that the herbaceous perennial mode of seasonal aestivation evolved early and lignification is a more recently derived trait and this may have negative effects on resprouting as the plant ages.

Key Words: burl, chaparral, fire, lignotuber, resprouting, sage scrub.

California shrublands are among the most fire-prone ecosystems in the world. The mediterranean-climate produces a seasonal distribution of precipitation and drought that are highly conducive to fire. Winter rains of typically 250–600 mm are coupled with cool winter temperatures that reduce evaporative loss and produce moist soil conditions that results in abundant primary production during the 4–6 mo growing season. The summer and fall dry season dries foliage sufficiently such that much of this growth is available fuel for fires. The extended dry season also favors shrubs over trees, and as a consequence much of the primary growth is maintained near the ground resulting in dense fuel packing, leading to high intensity stand-replacing crown fires that feed on canopies rather than surface litter. Growing season conditions also contribute to dense contiguous shrubland landscapes that further contribute to the spread of large wildfires. Today, most fires in California are anthropogenic in origin, however, prior to human entry into the region summer convection storms provided a source of ignitions. Although there is debate over the timing of the origin of the mediterranean climate, there is evidence that seasonal fire-type climates have been present in various parts of the world throughout the evolution of land plants (e.g., Glasspool et al. 2004; Cressler 2001; Falcon-Lang 2000; Scott and Stea 2002) and that fire was an important ecosystem process by at least the late Tertiary (e.g., Keeley and Rundel 2005).

Many plant traits have adaptive value in fire-prone environments, although debate remains as to which of these traits are true fire-adaptations, meaning they evolved in response to fire. In a crown-fire ecosystem, resprouting after top-kill is one such trait that is widely distributed in all mediterranean-climate shrublands of the world. The nearly ubiquitous distribution of resprouting in woody dicotyledonous plants (Wells 1969) suggests a very ancient origin, although this alone would not rule out fire as a primary driver since there is evidence that fire type environments have been present somewhere on the landscape throughout land plant evolution. Today, it is evident that resprouting has adaptive value following a variety of stresses including freezing (Mooney 1977) and grazing (Moreno and Oechel

1991), and thus it is perhaps prudent to think of resprouting as an adaptation to disturbance, and that fire was one of several selective agents. In some mediterranean-climate shrublands, resprouting is associated with enlarged basal tubers referred to as basal burls or lignotubers (James 1984). Although these more specialized resprouting structures show a marked association with mediterranean-climate shrublands, they are not characteristic of all resprouting species in those associations, and there is little consensus on their adaptive role (Keeley 1981; James 1984; Canadell and Zedler 1995).

Resprouting confers a marked advantage in rate of postfire recovery over species that regenerate entirely from seed (Keeley and Zedler 1978; Malanson and O'Leary 1982; Keeley and Keeley 1984; Tyler and D'Antonio 1995). However, the predictability of this advantage varies markedly between species. Some evergreen chaparral shrubs, including *Quercus berberidifolia*, *Heteromeles arbutifolia*, and *Malosma laurina*, are usually just top-killed and commonly 90–100% of the rootcrowns survive and resprout (Keeley et al. 2006). Others, such as "resprouting species" of *Arctostaphylos* and *Ceanothus* (subgenus *Ceanothus*), and the widespread *Adenostoma fasciculatum* may have a substantial portion of the population completely killed; in the latter species mortality varies from 0–100%, but typically is <50% (Rundel et al. 1987; Keeley et al. 2006). Likewise, the smaller stature semi-deciduous sage scrub exhibits marked differences between species in mortality and subsequent resprouting success, varying between 1–50% of the population (Keeley and Keeley 1984; Keeley et al. 2006).

Five factors have been hypothesized to explain differences in resprouting success: i) fire intensity, ii) plant size and biomass, iii) stem age, iv) seasonal differences in physiological condition, and v) fire frequency effects on plant condition. These are not mutually exclusive hypotheses and potentially more than a single factor is important in any given instance. It is likely that the importance of each varies spatially and temporally, as well as taxonomically.

A number of studies support the contention that fire intensity, which is the energy output of the fire, is one of the more important factors in shrub resprouting. Direct measures of fire intensity have shown effects on density of *Adenostoma fasciculatum* (chamise) resprouting stems (Moreno and Oechel 1994). Mortality of *A. fasciculatum* shrubs also has been shown to increase with increased fuel loading, presumably due to increased fire intensity (Moreno and Oechel 1994). Since fire intensity measures are usually only available for prescribed fires, most studies of wildfires use surrogates for fire intensity such as biomass loss, which are considered to be metrics of fire severity; e.g., Moreno and Oechel (1989) and Perez and Moreno (1998) have reported a significant relationship between heat output from a fire and the diameter of the smallest twig remaining on the shrub skeleton. Using this measure of fire severity there is a negative relationship with survival of resprouting shrubs and subshrubs ($r^2 = 0.17$, $P < 0.001$, n = 90 sites; Keeley unpublished analysis of data reported on in Keeley et al. 2005, 2006).

Rundel et al. (1987) found that plant size (measured by the aboveground lignotuber area) is a critical factor in postfire survival of resprouting *A. fasciculatum*, as has been noted for other chaparral shrubs (Keeley and Zedler 1978; Moreno and Oechel 1993), but other studies have failed to find such a relationship (Anfuso 1982; Stohlgren 1985). Although not tested in the context of fire, it has been reported that plant age may be an important factor in resprouting of the coastal scrub species *Baccharis pilularis* following cutting (Hobbs and Mooney 1985).

Seasonal effects on mortality and subsequent resprouting have also been documented and it appears that springtime depletion in rootcrown carbohydrate stores may be the primary factor in causing reduced resprouting success at this time (Laude et at. 1961; Parker 1987; Rundel et al. 1987; Beyers and Wakeman 2000). High fire frequency when repeat fires occur only a few years apart also is known to reduced resprouting success (Zedler et al. 1983; Haidinger and Keeley 1993), perhaps due to reduced recovery time for replenishment of rootcrown carbohydrates.

The purpose of this study was to examine patterns of fire-caused mortality and test the relative importance of fire severity and plant age across various shrubs and subshrubs characteristic of chaparral and sage scrub associations. In order to eliminate seasonal effects, I have studied sites that all burned during mid-autumn and during the same year.

METHODS

Ninety study sites were selected from 16 fires that burned over 80,000 ha across an area of more than 10,000 km^2 in southern California USA in late October and early November 1993 (further details in Keeley et al. 2005). Roughly comparable numbers of apparently low and high severity fires, and of chaparral and sage scrub sites were selected. Sampling was in spring 1994 and precipitation during this first growing season was only 80% of the long-term average for the region. Sampling was done in 20 × 50 m (tenth ha) sites with 10 nested 100-m^2 square subplots. Prefire woody plant density was based on a census of skeletal remains of shrubs and subshrubs in each subplot. All skeletons were recorded by species, which were identifiable based on form,

TABLE 1. COMPARISON OF DEAD AND RESPROUTING SHRUB SKELETONS FOR CHAPARRAL AND SAGE SCRUB RESPROUTING SPECIES. *** $P < 0.001$, *$P < 0.05$, ^{ns} $P > 0.05$. fs = facultative seeder, or = obligate resprouter.

	Mode	Skeleton height (cm)			Skeleton basal diameter (mm)		
		Dead (n)	Resprouts (n)	t-value P	Dead	Resprouts	t-value P
Shrubs							
Adenostoma fasciculatum	(fs)	37.6 (873)	102.4 (1467)	−28.091***	31.4	32.0	-0.828^{ns}
Adenostoma sparsifolium	(or)	102.3 (19)	235.8 (116)	−6.119***	43.6	61.4	−3.076*
Arctostaphylos spp.	(fs)	17.7 (44)	67.5 (24)	−4.246***	40.5	33.6	1.729^{ns}
Ceanothus spinosus	(fs)	56.1 (135)	202.9 (197)	−11.106***	48.1	53.9	-1.323^{ns}
Malosma laurina	(fs)	34.5 (23)	63.6 (585)	-1.954^{ns}	48.0	38.7	1.325^{ns}
Quercus berberidifolia	(or)	102.5 (16)	174.9 (296)	−2.774*	45.1	46.1	-0.291^{ns}
Rhus integrifolia	(fs)	12.8 (168)	105.1 (365)	−17.029***	49.6	69.5	−7.161***
Subshrubs							
Artemisia californica	(fs)	18.3 (958)	32.2 (410)	−6.438***	32.2	11.7	32.912***
Eriogonum fasciculatum	(fs)	6.4 (1489)	7.6 (247)	-1.038^{ns}	24.6	9.1	30.895***
Salvia apiana	(fs)	12.7 (201)	24.6 (333)	−6.323***	22.5	21.9	0.561^{ns}
S. leucophylla	(fs)	42.2 (116)	46.2 (276)	-0.905^{ns}	33.4	19.8	8.544***
S. mellifera	(fs)	17.9 (973)	52.0 (182)	−10.601***	33.9	20.7	14.806***

branching pattern, and bark. On some sites, skeletons were burned to ground level but characteristics of root-crown shape allowed us, in most cases, to assign a species name. In a small percentage of cases (<1%), skeletal remains were unidentifiable to species. These skeleton populations are inferred to represent the prefire shrub population density; however, I lack a measure of the amount of error associated with this method. In general, skeletons at densities and spacing similar to that observed in unburned stands were observed and so I assumed that they represented an acceptable estimate of the prefire population of living shrubs. It seems likely that this estimate comprises mostly living shrubs prior to the fire, as dead shrubs would be more likely to be completely consumed by fire and not leave a recognizable skeleton. Nomenclature is according to (Hickman 1993).

Because these were wildfires and covered large areas, direct measures of fire intensity were unavailable. I used a measure of biomass loss as a surrogate for fire intensity that is best referred to as a measure of fire severity. This measure of fire severity is justified since fire intensity is defined by the amount of biomass consumed (e.g., Byrum 1959). Our metric was the height of the shrub or subshrub skeleton, measured for 5 skeletons of each species in the subplots. Because of the even-aged nature of these crown-fire ecosystems, most shrubs are approximately the same height in mature communities and this is even more so within the same species. Thus, it was assumed that height of the skeleton was inversely related to fire intensity. Since there are no prior studies relating shrub skeleton height to fire intensity, we used least squares regression to evaluate the correlation between average skeleton height at a site with diameter of the smallest twig on skeletons, which is a parameter that has been shown to correlate with fire intensity (e.g., Moreno and Oechel 1989).

In order to examine the relationship between resprouting success and plant age, and obtain large samples of all dominant species, we were not able to age each individual shrub. Therefore, we assumed that age was correlated with basal diameter of the largest prefire stem, so basal diameter was measured with calipers on these same 5 skeletons.

Initial analysis showed that skeleton characteristics roughly followed a normal distribution of sizes. Thus, statistical comparisons between dead and resprouted plants were done with a two-tailed pooled t-test.

RESULTS

Resprouting success varied from about 10% for *Eriogonum fasciculatum* (average of 36 sites) to a high of 98% for *Quercus berberidifolia* (average of 6 sites). In order to relate resprouting shrub survivorship to fire severity (a surrogate for fire intensity) we used height of the remaining shrub skeleton for each shrub. Using site averages for skeleton height and diameter of the smallest twig on skeletons we found a significant relationship between these two measures ($r^2 = 0.24$, $P < 0.001$, $n = 90$); since the twig diameter has been shown to correlate with fire intensity (Moreno and Oechel 1989) we infer skeleton height is a measure of fire intensity. Skeleton characteristics of resprouting versus dead individuals for the 12 most abundant species are shown in Table 1. For most of the shrub species, skeletons of resprouting plants were significantly taller than those of dead individuals of the same species, indicating lower severity (intensity) fires

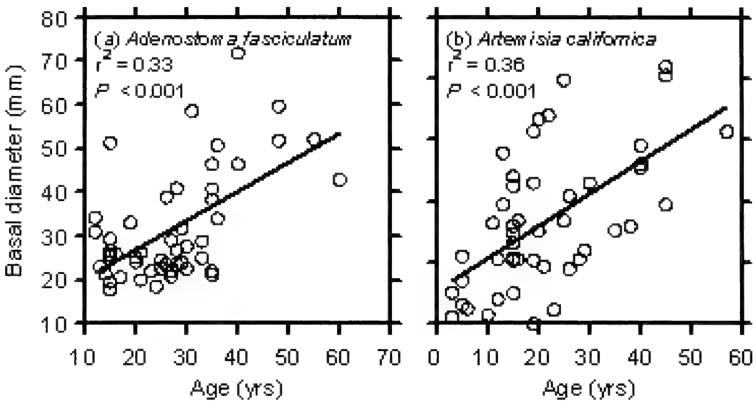

FIG. 1. Relationship between basal diameter of postfire skeletons and prefire stand age for one of the most widely distributed (a) shrubs in this study, *Adenostoma fasciculatum* (chamise), found at 50 sites and (b) subshrubs, *Artemisia californica* (California sagebrush), found at 47 sites.

were associated with resprouting success. This pattern was less strongly the case with sage scrub species; two of the five species exhibited no relationship between measures of fire severity and resprouting.

In order to relate resprouting to plant age, we depended upon the basal diameter of the largest stem on skeletons as a surrogate for plant age. This assumption is supported by the significant relationship between basal diameter and stand age for the most widely distributed shrub (Fig. 1a) and subshrub (Fig. 1b). Shrubs and subshrubs differed markedly in the effect of plant age (as estimated by basal diameter) on resprouting success (Table 1). For most shrubs, age was not related to resprouting ability, whereas in four out of five subshrub species it was. Particularly surprising is the fact that for subshrubs the youngest individuals with the smallest diameter stems (see for example, Fig. 2a) had a significantly greater likelihood of sprouting than older larger subshrubs (e.g., Fig. 2b).

DISCUSSION

Differential resprouting is likely a function of both innate characteristics of species as well as environmental variation during and after fire. Physiological status of storage carbohydrates has been implicated in seasonal differences in resprouting behavior (Radosevich and Conard 1980; Rundel et al. 1987), but that is not a factor in the differential survivorship of resprouters in this study since all sites burned in the same 10-day period (Keeley et al. 2005).

Fire intensity has often been invoked to explain mortality of resprouting shrubs (Moreno and Oechel 1991, 1994). In the present study, based on the premise that skeleton height is a reflection of fire intensity, there is evidence that for most shrubs, fire intensity is an important determinant of mortality (Table 1).

Alternatively, some have found that plant size, in particular rootcrown or lignotuber area is important in resprouting ability with older plants more likely to survive and resprout (Stohlgren 1985; Moreno and Oechel 1991; Vesk et al. 2004). In the present study, I have not considered this variable since sage scrub species generally lack a distinct lignotuber and don't form massive rootcrowns as is the case with some chaparral species.

A variable distinct from that of rootcrown size is the age of the aboveground plant, or in other words time since last fire. In chaparral shrubs, age does not play an obvious role in determining mortality vs resprouting. However, of particular interest is that in sage scrub subshrubs, resprouting is inversely related to plant age, and thus is more likely in younger plants (Table 1). For two common sage scrub subshrubs, *Artemisia californica and Eriogonum fasciculatum*, plants that resprouted typically had skeleton basal diameters of 1 cm or less (e.g., Fig. 2a). These were the largest stems on the plant and likely are indicative of plants a decade old or less. Plants with much larger diameter stems (e.g., Fig. 2b) typically did not resprout after fire. *Salvia mellifera and S. leucophylla* were other subshrubs on our sites that exhibited a similar pattern (Table 1). This pattern also has been reported before for the north coastal scrub subshrub *Baccharis pilularis* (Hobbs and Mooney 1985).

I hypothesize that the reason for this inverse relationship between age and resprouting in certain sage scrub species is that as these subshrubs age, there is a tendency to loose the resprouting ability. In the case of *Baccharis pilularis*, Hobbs and Mooney (1985) found that the mechanism behind this loss was that as the plant aged, adventitious buds responsible for sprouting, became buried by woody tissues, and this prevented older shrubs from resprouting.

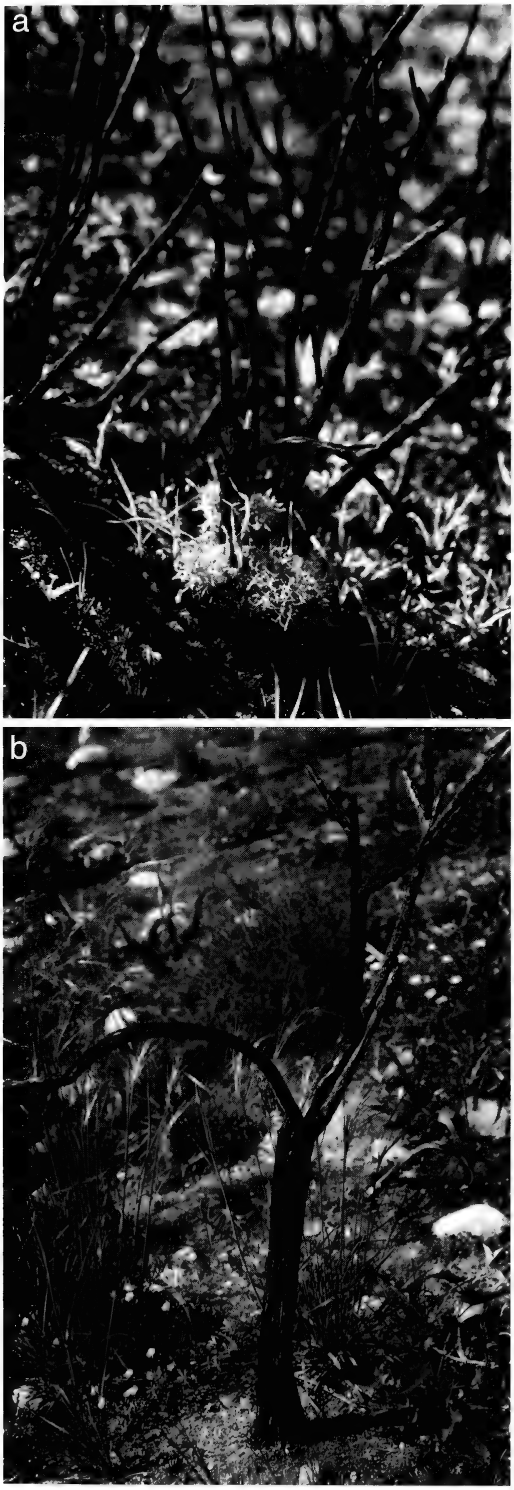

FIG. 2. First postfire year *Artemisia californica* skeletons; (a) a subshrub with prefire stem diameters <1 cm and estimated age of <5 yr that has resprouted and (b) with a basal stem diameter ca. 5 cm and an estimated age of >15 yr that was fire-killed and failed to resprout.

It is unknown if this is the mechanism responsible for the inverse age-resprouting pattern in *Artemisia californica* and *Eriogonum fasciculatum*.

I believe the age resprouting relationship differences between chaparral shrubs and sage scrub subshrubs is due to marked phylogenetic differences of the dominants. In the evergreen chaparral shrub genera of *Adenostoma*, *Malosma*, *Quercus*, *Rhamnus* and *Rhus*, all taxa are woody resprouters, as are all closely related sister genera, suggesting these are pleisomorphic traits, and the combination of woodiness and resprouting are rather ancient in these lineages.

In contrast, the sage scrub subshrubs in *Artemisia* (Asteraceae), *Baccharis* (Asteraceae), *Eriogonum* (Polygonaceae) and *Salvia* (Lamiaceae) are from largely herbaceous perennial genera and families. I hypothesize that in these lineages the herbaceous perennial mode of seasonal aestivation evolved early and lignification is a more recently derived trait. Seasonal aestivation results in aboveground die-back each dry season and resprouting from underground corms, bulbs and rhizomes the following growing season. In light of the fact that fires occur during the dormant season, it is not surprising that the vast majority of the herbaceous perennials in our shrublands are obligate resprouters (Keeley 2000). I hypothesize that resprouting is the basal condition in these lineages and secondary lignification has resulted in reduced allocation of resources to underground storage organs and increased concentration of adventitious buds in aboveground structures. As documented for *Baccharis piluarlis* (Hobbs and Mooney 1985), it is hypothesized that the increased lignification in sage scrub subshrubs has diminished resprouting ability due to the inhibitory effect of burying adventitious buds.

Based on patterns of character evolution in these lineages, the herbaceous perennial mode of seasonal aestivation does indeed appear to have evolved early and lignification is a more recently derived trait. For example, Frye and Kron (2003) mapped characters onto a molecular based phylogeny for the Polygonaceae. They found evidence that the herbaceous perennial mode of seasonal aestivation evolved early in the history of the family and the woody habit was derived multiple times within the group; in eight genera including *Eriogonum*. Likewise, Carlquist (2003) studied wood anatomy of this family and also concluded that woodiness arose secondarily in the genus *Eriogonum*. Based on a variety of evidence there is also support for both *Artemisia californica* and *Salvia* spp. subshrubs being in genera where the basal condition was herbaceous perennials and woodiness is a derived state (Torrell et al. 1999; Wang 2004; Walker *et al.* 2004).

Thus, secondary lignification in certain sage scrub subshrubs apparently has carried with it a cost of burying adventitious buds and diminishing the resprouting capacity. As a consequence, these subshrubs are most likely to resprout when in a developmental stage most closely resembling their herbaceous perennial ancestry.

Acknowledgments

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GENETIC RELATIONSHIPS AMONG *FREMONTODENDRON* (STERCULIACEAE) POPULATIONS OF THE CENTRAL SIERRA NEVADA FOOTHILLS OF CALIFORNIA

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ABSTRACT

Fremontias, or flannel bushes (*Fremontodendron*), are a distinctive element of California's chaparral communities. *Fremontodendron decumbens* is only known from a few populations in gabbro soil plant communities of the Sierra Nevada foothills in El Dorado County. Although a recovery plan for these communities has been drafted, the long-term management of *F. decumbens* is complicated by its treatment as a subspecies of the more widespread *F. californicum*, and by the recent discovery of additional populations of decumbent plants in Yuba and Nevada Counties that are not easily assigned to either *F. californicum* or *F. decumbens*. Genetic relationships among 5 populations, including *F. californicum*, *F. decumbens*, and the decumbent plants in Yuba County, were ascertained using AFLP markers. Principal coordinates and population structure analyses of the AFLP data showed that *F. decumbens* is genetically distinguishable from the populations of *F. californicum* that we sampled. This distinction, coupled with its unique morphology and ecology, support the treatment of *F. decumbens* as a species and promote its continued conservation as a rare and unique element of plant communities on gabbro soils in the Sierra Nevada. The decumbent Yuba County population shared a number of alleles with *F. californicum* and *F. decumbens* and the analyses did not clearly distinguish its taxonomic relationships. It is possible that this population represents an historical hybrid between *F. californicum* and *F. decumbens*. A resolution of the taxonomic position of the decumbent Yuba County populations will require more thorough sampling of *F. californicum* but the presence of unique alleles in this population suggests that it also should be conserved.

Key Words: Fremontodendron, AFLPs, STRUCTURE, population genetics, conservation, gabbro soils.

The flannel bushes or fremontias (*Fremontodendron*) are a distinctive element of chaparral vegetation in the Sierra Nevada foothills and coastal ranges of California, extending to scattered locations in central and western Arizona and the northern Baja California of Mexico. Kelman (1991) recognized three species: *Fremontodendron californicum* (Torrey) Coville, *F. mexicanum* Davidson, and *F. decumbens* R.M. Lloyd. *Fremontodendron californicum* is the most widespread and polymorphic, while *F. mexicanum* is confined to southern California and the Baja California peninsula of Mexico. *Fremontodendron decumbens* is an endemic element of the unique gabbro soil plant communities of the Sierra Nevada foothills, and was described from a population on the Pine Hill formation in El Dorado County (Lloyd 1965). It is known from only a few populations at this site, and was listed as federally endangered in 1996 (USFWS 1996) and included in a recovery plan for gabbro soil plants of the central Sierra Nevada foothills in 2002 (USFWS 2002). The long-term management of *F. decumbens* as an endangered species is complicated by two issues regarding its taxonomic rank: firstly by the treatment of *F. decumbens* as a subspecies of the more widespread *F. californicum* in the Jepson Manual (Hickman 1993), the primary reference for the California flora; and secondly by the discovery of other decumbent populations of *Fremontodendron* that are not assignable to *F. decumbens* on morphological grounds.

Diagnostic features of *F. decumbens* are its decumbent growth habit, orange to copper-red flowers (as opposed to the yellow flowers of *F. californicum* and *F. mexicanum*), dense stellate pubescence with long trichome rays on the abaxial leaf surface, and long peduncles. Kelman (1991) noted the presence of *F. decumbens* plants 1 km from the population at the summit of Pine Hill, and a large population of *F. decumbens* is also present on the eastern boundary of the Pine Hill Ecological Reserve (Boyd 2003). Beyond the Pine Hill site, decumbent plants of *Fremontodendron* have been collected from a number of localities in Yuba, Butte, and Nevada Counties. G. L. Stebbins collected plants from a population at a city dump site near Dobbins, Yuba County in 1966. An occurrence of decumbent *Fremontodendron*, with "deeper orange and smaller and more campanulate" flowers was noted by Campbell (1980) at a roadside locality near Campton-

TABLE 1. MEAN AND STANDARD ERROR (IN BRACKETS) FOR DIAGNOSTIC MORPHOLOGICAL CHARACTERS OF *FREMONTODENDRON* POPULATIONS. [1] Data from Kelman (1991), [2] Measurements of 10 shrubs grown at Canberra, Australia, [3] Basal branches well developed, plants as wide as tall.

	F. californicum[1]	*F. decumbens*[1]	*F.* "Yuba County"[2]
	n = 49	n = 48	n = 10
Habit	erect	decumbent[3]	decumbent
Leaf length (mm)	42 (9)	32 (8)	27 (6)
Leaf width (mm)	25 (10)	25 (7)	27 (10)
Trichome ray length (mm)	0.34 (0.19)	0.76 (0.14)	0.47 (0.10)
Flower color	yellow	orange to mostly copper-red	orange
Flower diameter (mm)	46 (8)	41 (6)	26 (5)
Peduncle length (mm)	9 (2)	17 (4)	6 (2)

ville, Yuba County. In 1975, Lowell Ahart collected plants from a population at a dump site near Brownsville, Yuba County. Later observations of this population indicated that although the plants were uniformly decumbent, the pale orange to yellow flower color and shorter peduncles argued against their assignment to *F. decumbens* (Table 1). In Butte County, Ahart collected plants from a site on the Bloomer Road, east of Lake Oroville. This population was described in the Manual of Vascular Plants of Butte County as "low and stunted but apparently not the ssp. *decumbens* (R.M. Lloyd) Munz … known only from Eldorado and Nevada counties". In 1985, a small population of decumbent plants was reported near Grass Valley in Nevada County (Marcia Braga personal communication). Using the diagnostic characters, these plants were not assignable to *F. decumbens* in that flower color was not as deep orange and the peduncles and trichome rays were not as long as those in *F. decumbens* measured by Kelman (1991) (Table 1). Because these new decumbent populations are not assignable to either *F. decumbens* or *F. californicum* based on leaf length, trichome ray length and flower color, their taxonomic status remains undetermined.

A fundamental question concerning the conservation management of *F. decumbens* is whether it represents a distinct taxon or is merely an ecotype of *F. californicum*, as implied by the transfer of *F. decumbens* to *F. californicum* by Munz (1968). Likewise, the management of the newly identified decumbent populations depends on whether they are assigned to *F. californicum*, *F. decumbens*, or a new taxon. This problem was emphasized in the recovery plan for Gabbro Soil Plants of the Central Sierra Nevada Foothills (USFWS 2002), which recommended that "the decumbent *Fremontodendron* within Nevada and Yuba Counties should be secured and protected unless they are determined not to be the listed [*F. decumbens*]." Since morphological evidence has not provided a clear answer to the species placement of the decumbent plants in Yuba County, molecular markers were used to clarify the genetic relationships among *F. decumbens*, *F. californicum*, and the decumbent population near Brownsville, Yuba County, and so provide a stronger basis for conservation decisions affecting these taxa.

METHODS

Leaf Sample Collection

The localities of the five populations are shown in Fig. 1. *Fremontodendron decumbens* leaf samples were collected from eight shrubs in the Pine Hill (PH) area of El Dorado County, all of which were within 150 m of each other. A further nine plants were sampled from a nearby population approximately 0.8 km north of Pine Hill (BLM), all within 20 m of each other. *Fremontodendron californicum* leaves were collected from eight plants on Tollhouse Road, Fresno County (THRD) and seven plants on Highway 168, Fresno County (HWY168); the sites are approximately 2.5 km apart. The "Yuba County" leaves were sampled from nine shrubs from the population near Brownsville, Yuba County (Yuba) mentioned in the introduction. Four additional samples were obtained from shrubs that were grown in Canberra, Australia, from seed of the same Yuba County population, accessed as Commonwealth Plant Introductions (CPI 140372, CPI 140375, CPI 140376, and CPI 140378). Leaves were preserved using silica gel or lyophilized prior to DNA extraction.

DNA Extraction and AFLP Procedures

Total genomic DNA was extracted using 10 mg of dried leaf tissue ground to a fine powder using 3 mm tungsten carbide beads in a Retsch MM300 mixer mill and extracted using the Qiagen 96-well DNEasy Extraction Kit (Qiagen, Melbourne). Amplified marker length polymorphism (AFLP™) templates were prepared and selectively amplified using three AFLP primer combinations (*E*-AGC:*M*-CAT, *E*-AGG:*M*-CTC, *E*-AGG:*M*-CTG) following Brubaker and Brown (2003). The *Eco*I-ANN primer was end-labeled with [^{33}P]-dATP and the AFLPs

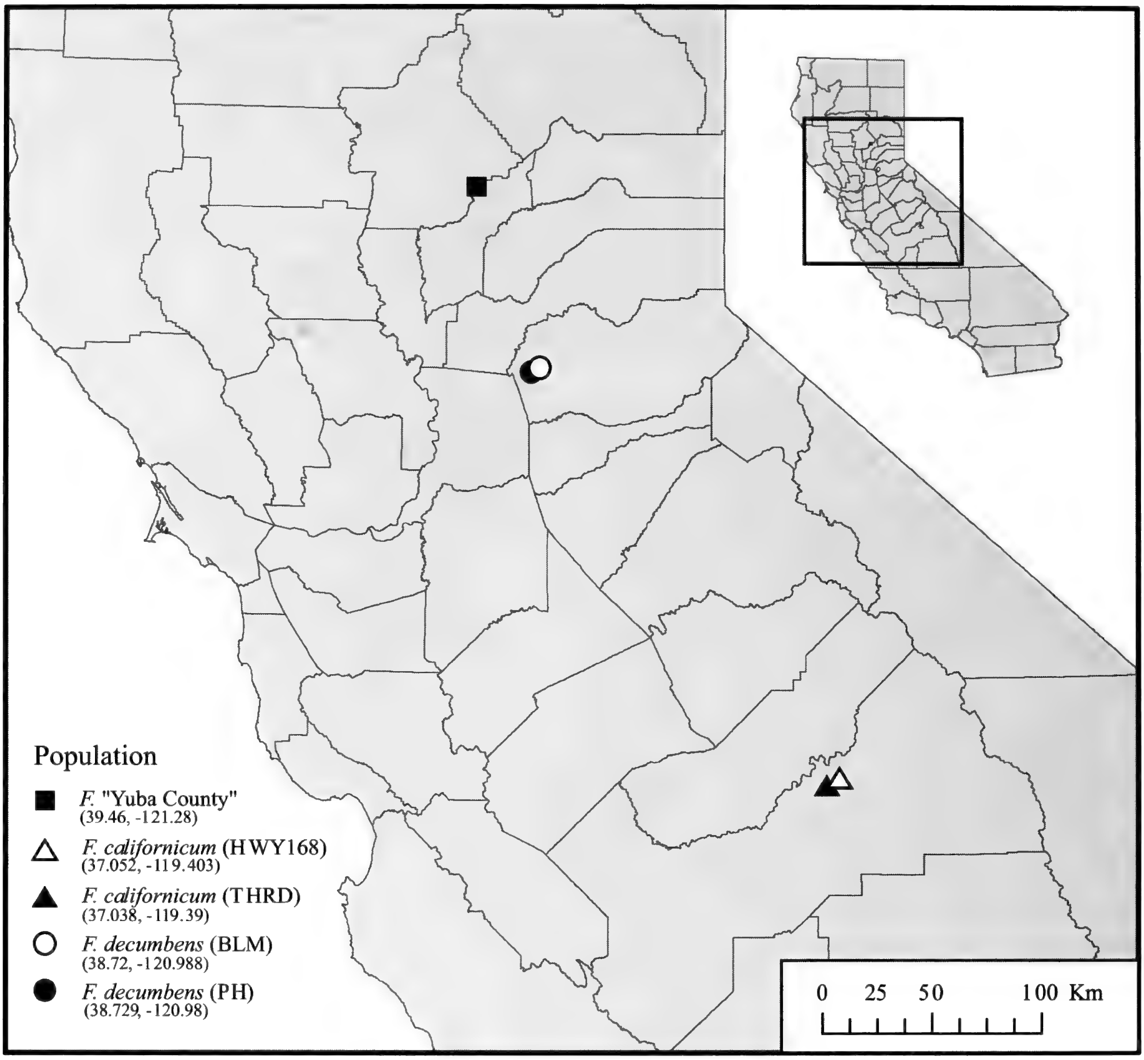

FIG. 1. Location of *Fremontodendron californicum*, *F. decumbens*, and *F.* "Yuba County" populations sampled.

were resolved on 6% denaturing polyacrylamide gels run at 50 watts using 1X Tris-Taurine-EDTA (TTE) buffer (following Brubaker and Brown 2003). The polyacrylamide gels were dried to the short plate and exposed to BiomaxMR (Kodak) film for one to four days. Autoradiograms were scored for the presence/absence of a total of 66 polymorphic AFLP loci that were numbered sequentially from largest to smallest.

Data Analyses

Allele frequencies were calculated with AFLP-SURV Version 1.0 (Vekemans 2002) using a Bayesian approach that assumed Hardy-Weinberg (H-W) genotypic proportions with non-uniform prior distribution of allele frequencies (Zhivotovsky 1999) and used to estimate average heterozygosity (Hj) which is analogous to gene diversity (H_e), the proportion of polymorphic loci (P), expressed as a percentage at the 5% level as well as total gene diversity (H_t) and genetic diversity within populations (sites) (H_s). Genetic differentiation among populations was assessed using Wright's F_{ST} following Lynch and Milligan (1994) with the confidence intervals (CI) estimated following 1000 permutations. Estimates of the pairwise relatedness coefficients between individuals (r) were calculated using AFLP-SURV following Lynch & Milligan's Taylor expansion (Lynch and Milligan 1994) and the relatedness matrix produced was used to extract and plot the first two principal coordinates (PCO). Nei's (1978) genetic distance (D) was calculated between population pairs using POPGENE (Yeh and Boyle 1997) and a UPGMA dendrogram was constructed using NTSYS 2.11X (Rohlf 2005).

TABLE 2. GENETIC DIVERSITY IN *FREMONTODENDRON* POPULATIONS ASSESSED USING AFLPS. (n = number of individuals genotyped; P = percentage of polymorphic loci; H_e = Gene Diversity)

Taxon	Population	n	P	H_e	Private Alleles
F. decumbens	BLM	9	22.2	0.120	1
	PH	8	75.9	0.274	
F. californicum	THRD	8	74.1	0.228	2
	HWY	7	63.0	0.222	
F. "Yuba County"	Yuba	13	72.2	0.284	5

Differentiation among populations and species was also assessed using STRUCTURE Version 2.1, which is a model-based clustering method for inferring population structure (Pritchard et al. 2000). In the first stage of the analyses, the two *F. californicum* and the two *F. decumbens* populations were analyzed without using any prior information to determine the most likely number of sub-populations (K). Following this, individuals within each species were reassigned to their most likely sub-population and the origin of the "Yuba County" individuals was inferred relative to this genetic background. All analyses were conducted using a 30,000 burn-in and 300,000 runs and were replicated five times.

RESULTS

Levels of genetic diversity varied among the populations (Table 2). The *F. decumbens* BLM population had the fewest polymorphic loci (P = 22.2%) and lowest gene diversity (H_e, 0.120) of all the populations sampled. Levels among the other populations were similar although the Yuba County population had the highest gene diversity (0.284), possibly reflecting the larger sample size of this population. Unique alleles were present in PH (1), THRD (2) and Yuba (5). The low level of genetic diversity in BLM arose from the fact that there were only three multilocus genotypes in the population. In contrast, all individuals in the other three populations were genetically dissimilar. Population differentiation indicated that most of the total genetic diversity (H_t = 0.307) was apportioned within sites (H_s = 0.226), with significant genetic differentiation among populations (F_{ST} = 0.263, $p < 0.001$).

The first principal co-ordinate placed the two *F. decumbens* populations in negative space while the *F. californicum* populations were in positive space (Fig. 2A). Almost all the Yuba County individuals ordinated in positive space with the *F. californicum* individuals along the first principal coordinate (Fig. 2A). As predicted by the F_{ST} value, genetic distances among the five populations were also high and long branch lengths separated *F. californicum* and *F. decumbens* in the UPGMA topology (Fig. 2B). The Yuba County individuals clustered with the *F. californicum* populations (Fig. 2B).

The genetic differentiation between the *F. californicum* and *F. decumbens* populations evident in the principal coordinates analysis was also apparent in the initial STRUCTURE analysis. The most likely number of inferred gene pools was four rather than two [mean *ln* P(D) of −473 versus −625]. Both taxa were clearly divided into two gene pools that were largely congruent with their population of origin (Fig. 3A). When the origins of the Yuba County individuals were inferred relative to this genetic background, it emerged as a genetically distinct element, a result that correlated with the high number of unique alleles present in this population (Table 2). Nonetheless, there were obvious genetic inputs to the Yuba County population from both *F. californicum* and *F. decumbens* (Fig. 3B), although the level of this influence varied substantially among individuals. The influence of *F. californicum* appeared to be greater than that of *F. decumbens*, a result consistent with the principal coordinates analysis, where the Yuba County individuals ordinated with *F. californicum* along the first axis (Fig. 2A). A structure analysis, in which no population information was used, produced a congruent result (i.e., there was unambiguous support for five distinct populations).

DISCUSSION

This study was prompted by uncertainty regarding the taxonomic rank of decumbent *Fremontodendron* populations and the consequences of this for their conservation management. As evident in Table 1, a number of diagnostic morphological features (in addition to habit) differentiate *F. decumbens* from *F. californicum*. The genetic evidence presented here using measures of genetic distance (Fig. 2B) and population structure (Fig. 3A) also clearly separates the two species. A taxonomic treatment that merges these populations in a single species belies the genetic, morphological, and ecological discrimination between the two taxa and weakens the case for the conservation of the *F. decumbens* populations of El Dorado County.

Species with restricted distributions, such as *F. decumbens*, generally exhibit lower levels of genetic diversity than their more widespread

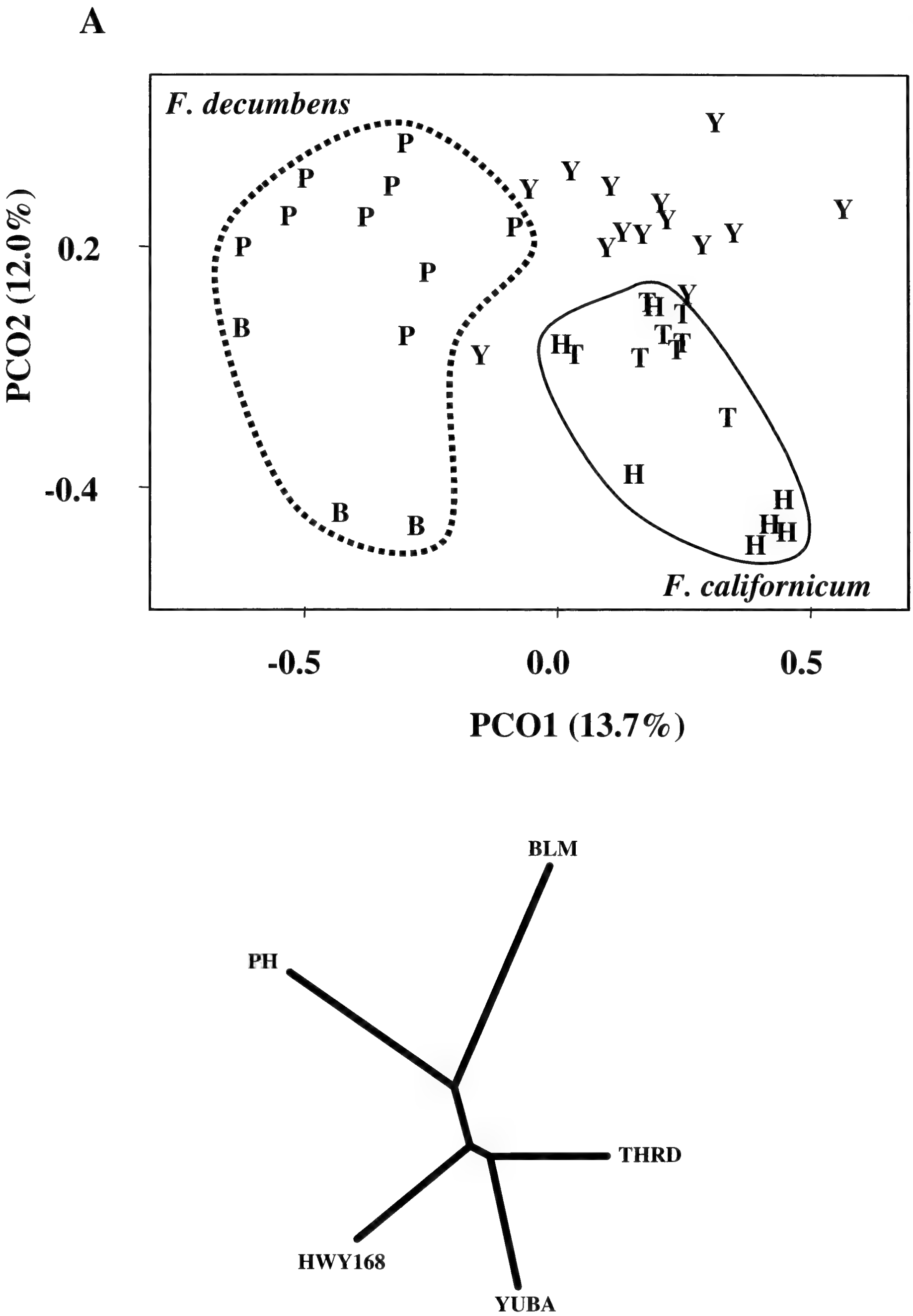

FIG. 2. A. Principal coordinates analysis of *F. decumbens* (P = PH, B = BLM), *F. californicum* (H = HWY168, T = THRD) and Yuba County (Y) individuals based on Lynch and Milligan's (1994) relatedness matrix. B. UPGMA topology based on Nei's (1978) genetic distance (*D*).

counterparts (Hamrick and Godt 1989; Gitzendanner and Soltis 2000), but this is not always the case and probably reflects the myriad of factors that can contribute to rarity (Karron 1987; Fiedler and Ahouse 1992). The *F. decumbens* PH population had the highest levels of genetic diversity of the two species indicating it is not genetically depauperate with respect to its widespread congener. However, further sampling of *F. californicum* is necessary to accurately quantify the differences in genetic diversity between the two species. In contrast, plants of the other *F. decumbens* population (BLM), which were within 20 m of one another, had substantially lower

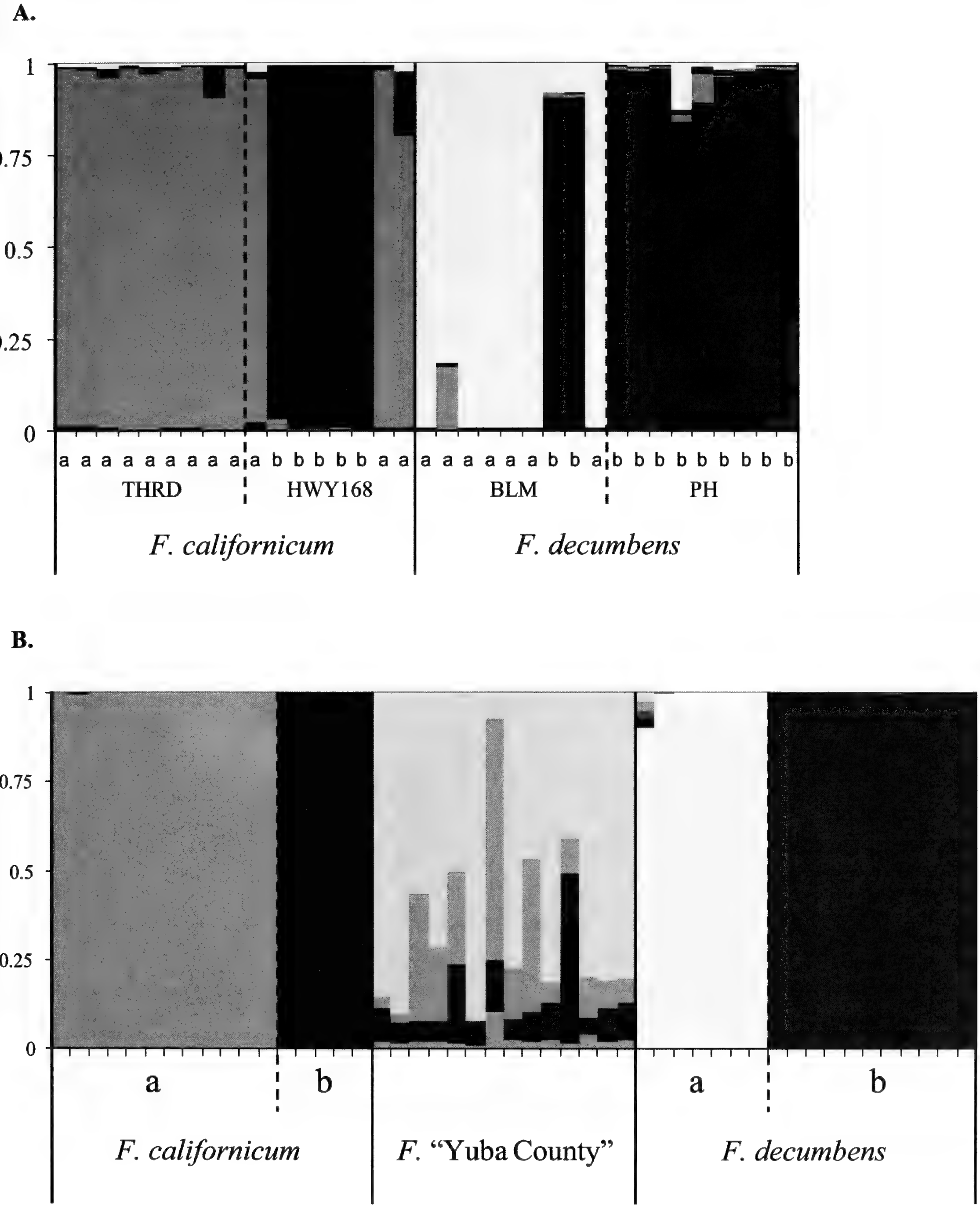

FIG. 3. Pictorial representation of the genetic structure among the five *Fremontodendron* populations generated using STRUCTURE (Pritchard et al. 2000). The different shades represent genetic subsets of the sampled populations. A. An analysis without the Yuba County individuals suggests that there are two distinct genepools within *F. decumbens* and within *F. californicum*, designated "a" and "b", respectively. B. Based on the first analysis, individuals were re-designated by their respective gene pools and the origins of the Yuba County individuals were assigned relative to *F. decumbens* and *F. californicum*.

levels of genetic diversity and a high level of relatedness among individuals. This may indicate a recent founder event, vegetative reproduction, or that genetic erosion and high levels of inbreeding have occurred. Although reduced heterozygosity can be deleterious to population fitness (Reed and Frankham 2003) and compromise the long term persistence of populations

through poor seed set, smaller seed, slower germination response, poor seedling survival, and reduced reproductive capacity (Buza et al. 2000; Oostermeijer 2000; Young et al. 2000; Tomimatsu and Ohara 2003), this is not always the case, particularly for self-fertile species. While further genetic and demographic investigation of the BLM population is warranted, habitat loss is probably the most critical short-term process to manage.

The taxonomic status of the more recently discovered decumbent populations found in Yuba and Nevada Counties is more difficult to resolve. They do not have the distinctive correlated characters of *F. decumbens* and on other morphological grounds would fall within the range of variation of *F. californicum*, and if it were not for their decumbent habit they would have been so treated. The genetic data for the Yuba County individuals is similarly ambiguous. In the ordination analysis, the Yuba County individuals grouped within a larger cluster of *F. californicum* individuals along the first axis, and there were genetic inputs to the Yuba population from *F. californicum* and *F. decumbens*. While a number of hypotheses could be formulated to explain these relationships, the most likely scenario is that the Yuba County population (and by inference the Nevada County population) is derived from an historical hybridization between *F. californicum* and *F. decumbens*. This could explain, in part, the higher levels of genetic diversity observed in the Yuba county population relative to *F. californicum* and *F. decumbens*. Hybridization is a common event in angiosperms and estimates of natural hybridization among plant taxa range from 6–22% worldwide (Ellstrand et al. 1996), primarily due to the semi-permeable nature of plant reproductive barriers (Harrison 1993). Hybridization can lead to increased intra-specific genetic diversity, the origin and transfer of genetic adaptations, the origin of new ecotypes or species, and the reinforcement or breakdown of reproductive barriers (see Rieseberg 1997). The unequal contributions of *F. californicum* and *F. decumbens* to the Yuba County population could be explained by subsequent backcrossing to the more widespread *F. californicum*. That the genetic makeup of the Yuba County individuals can not be ascribed simply to *F. californicum* and *F. decumbens* suggests that the actual parental populations may not have been sampled (particularly for *F. californicum*), or that the hybrid populations have existed long enough that backcrossing and directional selection has substantially shifted gene frequencies.

Our results do not support definitive conservation recommendations regarding the Yuba and Nevada County populations, but the presence of unique alleles in the Yuba County gene pool indicates that this population should be conserved until further data are available. The morphological similarity and spatial proximity between the Yuba and Nevada County decumbent populations predict they will be genetically similar. When the single Nevada County individual that we had access to was included in a separate principal coordinates analysis (not presented), it fell within the Yuba County cluster, but this population needs to be sampled more thoroughly before any robust conclusions can be made. As noted above, there is a strong possibility that the Yuba and Nevada County populations originated from hybridization. The conservation of hybrid populations is controversial since introgression can lead to species extinction (Allendorf et al. 2001). With increased fragmentation of natural habitats around the world, however, once rare hybrid events may become more common place and could threaten species integrity. The challenge for conservation managers is to determine whether hybridization events are natural or anthropogenic (Allendorf et al. 2001), and whether they pose a real threat. Like their cogener, *F. decumbens*, the distribution of the other northern decumbent populations appears to be associated with gabbro or ultramafic substrates. It is hard to envision how one or more anthropogenic hybridization events would result in the apparent substrate-specific distribution observed. If the decumbent populations share adaptation to these unusual substrates, this would be another indicator of a shared genetic heritage. Any proposed reintroduction of *F. decumbens* should not use the Yuba and Nevada County populations as sources of seed. Resolving their taxonomic status will require a more extensive sampling of *F. californicum* populations.

While an understanding of the levels and patterns of genetic diversity is an integral component of species management, ecological and evolutionary interactions should also be considered (Holsinger and Gottlieb 1991). *Fremontodendron decumbens* is pollinated by native bees (Boyd 1994), has seeds which are dispersed by ants (Boyd 1996) and suffers high reproductive attrition from insects and rodents (Boyd 2003). Furthermore, *F. decumbens* and the other decumbent populations are components of plant communities that have varying reestablishment strategies following fire (Marsh and Ayres 2002). These mutualistic and community relationships highlight the importance of conserving these populations as integral elements of the Sierra Nevada gabbro flora (USFWS 2002).

Acknowledgments

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CIRCUMSCRIPTION OF *ECHINOCEREUS ARIZONICUS* SUBSP. *ARIZONICUS*: PHENETIC ANALYSIS OF MORPHOLOGICAL CHARACTERS IN SECTION *TRIGLOCHIDIATUS* (CACTACEAE), PART II

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ABSTRACT

A multivariate analysis was performed for populations of *Echinocereus* (section *Triglochidiatus*) to facilitate the taxonomic circumscription of *E. arizonicus* subsp. *arizonicus*. Twenty-one morphological characters for 16 populations evidenced the validity of at least two subspecific taxa within *E. arizonicus*: *E. arizonicus* subsp. *arizonicus* and *E. arizonicus* subsp. *nigrihorridispinus*. Principle components analysis indicated that stem characters were most diagnostic in defining two distinct groups of populations, each including the type locality of one of the two subspecies. Unweighted pair group method with arithmetic mean (UPGMA) clustered populations of the two subspecies apart from one another and from those of the outgroup, *E. triglochidiatus* subsp. *mojavensis*. For most measured characters, means differed significantly between the two subspecies. Discriminant analysis correctly classified 97.0% for individuals of *E. arizonicus* subsp. *arizonicus* and 94.7% for individuals of *E. arizonicus* subsp. *nigrihorridispinus*, compared to an overall 97.8% correct classification of individuals for all perfect-flowered taxa of section *Triglochidiatus* investigated.

Key Words: *Echinocereus arizonicus*, section *Triglochidiatus*, multivariate analysis, morphological characters.

Taxonomy within section *Triglochidiatus* H. Bravo of *Echinocereus* Engelm. in F. A. Wislizenus has vacillated dramatically over the past few decades. The present study evaluates the circumscription of *E. arizonicus* Rose ex Orcutt subsp. *arizonicus* using multivariate techniques to compare morphological variation within populations to that among populations. It is the second portion of an ongoing phenetic analysis of section *Triglochidiatus*, the first of which addressed the recently discovered species, *E. yavapaiensis* M. A. Baker, and summarized the current knowledge of polyploidy within the section (Baker 2006). The taxonomic status of *E. arizonicus* subsp. *arizonicus*, which is federally listed as Endangered, has importance for conservation efforts because of threats from mining and other human related impacts.

Until recently, the most widely recognized treatment of *Echinocereus* was by Benson (1982), who grouped all of the red-flowered populations within the United States under a single species, *E. triglochidiatus* Engelm. in F. A. Wislizenus. Since Benson's treatment, other authors reported on the section (Taylor 1985; Ferguson 1989) but did not use biosystematic approaches. Recent taxonomic, cytological, and floral investigations have led specialists to separate Benson's North American *E. triglochidiatus* into at least five species, *E. arizonicus*, *E. coccineus* Engelm. in F. A. Wislizenus, *E. santaritensis* W. Blum & Rutow, *E. triglochidiatus*, and *E. yavapaiensis* M. A. Baker (Hoffman 1992; Blum et al. 1998; Zimmerman & Parfitt 2003; Baker 2006). The primary rationale for splitting *E. triglochidiatus* into several species is the occurrence of polyploidy correlated with morphology, geographic distribution, and floral dimorphism (Table 1). *Echinocereus arizonicus* represents smooth-spined, diploid, perfect-flowered populations from the Sonoran-Chihuahuan Desert interface; *E. triglochidiatus* represents papillate- [*E. triglochidiatus* subsp. *mojavensis* (Engelm. & Bigelow) W. Blum & Michael Lange] or angular-spined (*E. triglochidiatus* subsp. *triglochidiatus*), diploid, perfect-flowered, populations from the Mojave Desert, California east to northern New Mexico and north into Utah and Colorado; *E. coccineus* represents smooth to papillate-spined, tetraploid, florally dimorphic populations from southern Utah south into the mountains of Arizona and from southern Colorado south into Texas and southern Chihuahua; *E. santaritensis* W. Blum & Rutow represents tetraploid, perfect-flowered, populations from southern Arizona, and *E. yavapaiensis* hexaploid, florally dimorphic, populations from central Arizona. Several taxa endemic to Mexico remain poorly understood. For a synopsis of chromosome numbers in *Echinocereus*, section *Triglochidiatus*, see Cota and Philbrick (1994) and Baker (2006).

Nomenclature herein follows that of Blum et al. (1998). Three taxa are recognized within *E.*

TABLE 1. CURRENT TAXONOMIC STATUS OF *ECHINOCEREUS*, SECTION *TRIGLOCHIDIATUS* FOR POPULATIONS IN THE UNITED STATES AS RECOGNIZED BY ZIMMERMAN & PARFITT (2003) AND BAKER (2006).

Taxon	Spine surface	Ploidy level	Flowers	Status in the current multivariate analysis
E. arizonicus	smooth-spined	diploid	perfect	Analyzed
E. triglochidiatus subsp. *mojavensis*	papillate-spined	diploid	perfect	Analyzed as an outgroup
E. triglochidiatus subsp. *triglochidiatus*	angular-spined	diploid	perfect	Analyzed as an outgroup
E. santaritensis	smooth-spined	tetraploid	perfect	Analyzed as an outgroup
E. coccineus	smooth to papillate-spined	tetraploid	dimorphic	Not included, see Baker 2006
E. yavapaiensis	smooth-spined	hexaploid	dimorphic	Not included, see Baker 2006

arizonicus, *E. arizonicus* subsp. *arizonicus*, *E. arizonicus* subsp. *nigrihorridispinus* W. Blum & Rutow, and *E. arizonicus* subsp. *matudae* (Bravo-Hollis) Rutow. According to Blum et al. (1998), *E. arizonicus* subsp. *arizonicus* occurs in Cochise, Gila, Graham, Pima, and Pinal Counties, Arizona, and is characterized as having 7–13 radial spines and 1–4 central spines per areole and stems with 8–11 ribs; *E. arizonicus* subsp. *nigrihorridispinus* occurs in areas southeast of the distribution of *E. arizonicus* subsp. *arizonicus*, in southern Arizona, southwestern New Mexico, and northern Chihuahua and is characterized as having 10–14 radial spines and 3–8 central spines per areole and stems with 10–13 ribs; *E. arizonicus* subsp. *matudae* occurs northwestern Chihuahua and is characterized as having 7–11 radial spines and 1–4 central spines per areole and stems with 6–8 ribs.

METHODS

Twenty one continuous characters (Table 2) were measured for at least 30 mature individuals from six populations of *E. arizonicus*, two of *E. triglochidiatus* subsp. *triglochidiatus*, four of *E. triglochidiatus* subsp. *mojavensis*, and three of *E. santaritensis* (Fig. 1, Table 3). Because of permitting constraints, stem characters only were measured for the only known population of *E. arizonicus* subsp. *matudae* (Bravo-Hollis) Rutow. For statistical purposes, the assumption was made that all individuals measured within each population belonged within a single taxon. Although it is possible that individuals of more than one taxon occurred within the vicinity of any one study population, there were no locations where this was apparent from the physiognomy of the individuals present.

TABLE 2. LIST OF CHARACTERS USED IN THE ANALYSIS. Except for STEML, three measurements were made for each character per individual. The youngest fully mature areoles were chosen for stem measurements.

Character	Explanation
STEML	Length of longest stem from ground level
STEMDIA	Average stem diameter
NRIBS	Average number of stem ribs (costae)
DBTWARLS	Average distance between stem areoles
NCENTRALS	Average number of central spines per stem areole
NRADIALS	Average number of radial spines per stem areole
LRADIALS	Average length of radial spines per stem areole
LCENTRALS	Average length of central spines per stem areole
THKNCNTR	Greatest thickness of central spine (just above the swollen base) per stem areole
FLRL	Flower length from base of pericarp to tip of longest tepal
FLRWIDTH	Flower width from tepal tip to tepal tip
OUTSDIA	Outside diameter of throat of pericarp at constriction just above ovary
AXIALL	Axial length of pericarpal pith between ovary and base of pericarp
LTOUPPER	Length of pericarp from base to uppermost areole
NTEPALS	Number of tepals, excluding those with areoles at their base
STYLEDIA	Diameter of style at midpoint.
SPINEL	Length of longest within uppermost areole of pericarp
STYLEL	Length of style from its base to bottom of stigma
NCTRYDIA	Diameter of nectar chamber
OVARYL	Length of ovary
STAMENL	Length of stamens collectively

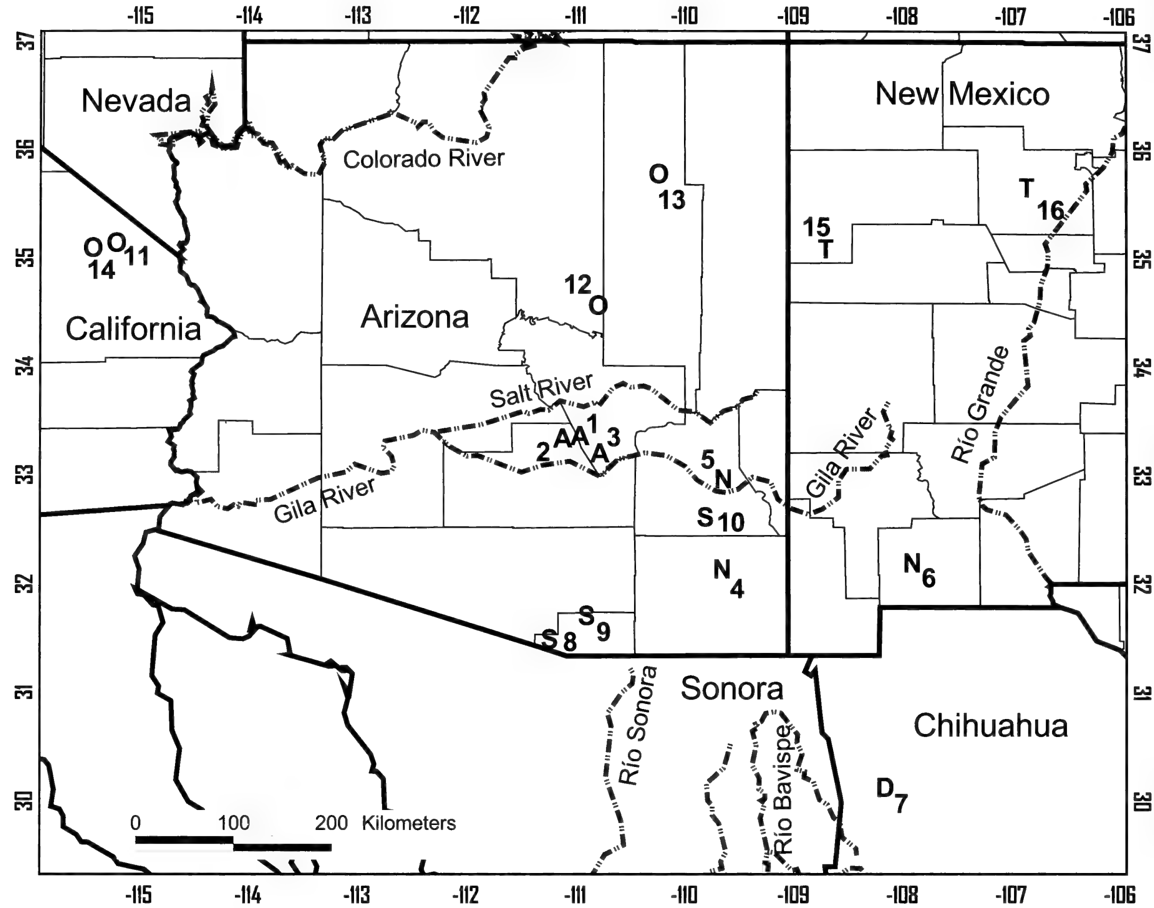

FIG. 1. Locations of study sites for populations of *Echinocereus* section *Triglochidiatus*. Numbers next to symbols refer to those of populations in Table 1.

Principle component analysis (PCA) (Systat7, SPPS Software Inc. 2000) was used to assess the taxonomic values of characters and to assign populations of Arizona and New Mexico populations of *E. arizonicus* to either *E. arizonicus* subsp. *arizonicus*, or *E. arizonicus* subsp. *nigrihorridispinus*. This was done by comparing individuals within unknown populations to those of the two type localities. In order to assess the taxonomic value of groups of variables (primarily stem characters vs. flower characters), PCA was first performed on all characters of populations of all three perfect-flowered species, and then performed using flower characters and stem characters alone. Varimax rotation was used to improve the interpretability of the scatter diagrams. The clustering algorithm unweighted pair group method with arithmetic mean (UPGMA) was performed with NTSYS® 2.1e (Rohlf 2000) to compare phenetic distance among populations of *E. arizonicus* and the outgroup, *E. triglochidiatus* subsp. *mojavensis*. This outgroup was selected because it was the only other diploid taxon for which at least three populations had been measured.

MANOVA (SPSS10) was used to test the assumptions of multivariate statistics and to test the significance of characters among taxa. Data were transformed, as necessary, to meet multivariate assumptions. Not all variables met homogeneity of variance assumptions after transformations. Also, the assumption of homogeneity of covariance matrices could not be met (Box's M test, $P < 0.001$). The Box's M test, however, is generally too strict with the large sample sizes generally necessary for multivariate applications of ANOVA (Tabachnick 2001).

Discriminant analysis (DA; SPSS10) was used to test for the correct classification of individuals within their respective taxa. Because of the small sample size, individuals of *E. arizonicus* subsp. *matudae* were not included in the analysis. Nine individuals were identified as multivariate outliers (Mahalanobis distance-squares from group means with $P < 0.001$) and were deleted from the analysis. A permit (TE-844147) for collecting flowers from individuals of *E. arizonicus* was issued by the U. S. Fish and Wildlife Service, Southwest Regional Office, Albuqerque, New Mexico.

TABLE 3. LOCATIONS OF POPULATIONS (TYPE LOCALITIES IN BOLD, CHROMOSOME DETERMINATIONS FROM BAKER [2006]).

Pop. No.	Taxon	Locale	*n*	Latitude, longitude	Elev. (m)	Collector and number
1	*E. arizonicus* subsp. *arizonicus*	**Top of the World, Gila CO., AZ**	11	33° 21.3′ 110° 58.4′	1395	*MAB 13781.1*
2	*E. arizonicus* subsp. *arizonicus*	N of Oak Flat, Pinal Co., AZ	11	33° 20.5′ 111° 02.3′	1400	*MAB 13782.1*
3	*E. arizonicus* subsp. *arizonicus*	El Capitan, Gila Co., AZ	11	33° 12′ 110° 47′	1600	*MAB 13803*
4	*E. arizonicus* subsp. *nigrihorridispinus*	Dos Cabezas, Cochise Co., AZ	11	32° 10.7′ 109° 38.9′	1500	*MAB 13748, 13749*
5	*E. arizonicus* subsp. *nigrihorridispinus*	N of Safford, Graham Co., AZ	11	32° 59′ 109° 39′	1460	*MAB 11623*
6	*E. arizonicus* subsp. *nigrihorridispinus*	**W of Deming, Luna Co., NM**	11	32° 13′ 107° 54	1460	*MAB 13958*
7	*E. arizonicus* subsp. *matudae*	**Casa Grandes, Chihuahua, Mexico**	11	30° 08.3′ 108° 09.6′	2200	*MAB 14339.1*
8	*E. santaritensis*	Ruby, Santa Cruz Co., AZ	22	31° 28.1′ 111° 13.5′	1360	*MAB 13422*
9	*E. santaritensis*	**Madera Canyon, Santa Cruz Co., AZ**	22	31° 42.7–43.7′ 110° 52.3–53.9	1480–2210	*MAB 13734, 13736, 13737, 13783*
10	E. santaritensis	Mt. Graham, Graham Co., AZ	22	32° 37′ 109° 49′	2525	*MAB* 13810
11	*E. triglochidiatus* subsp. *mojavensis*	**N of Hackberry Mtn., San Bernardino Co., CA**	11	35° 09.3′ 115° 13.4′	1335	*MAB 13706*
12	*E. triglochidiatus* subsp. *mojavensis*	Chevelon Canyon, Coconino Co., AZ	11	34° 35.6′ 110° 47.4′	1950	*MAB 13792*
13	*E. triglochidiatus* subsp. *mojavensis*	Keams Canyon, Navajo Co., AZ	11	35° 47′ 110° 14′	1895	*MAB 13626*, 13796
14	*E. triglochidiatus* subsp. *mojavensis*	**Black Canyon, San Bernardino Co., California. (type locality of E. sandersii Orcutt**	11	35° 07′ 115° 24′	1600	*MAB 13957*
15	*E. triglochidiatus* subsp. *triglochidiatus*	**Zuni, McKinley Co., NM (type locality of C. gonacanthus)**	11	35° 04.5′ 108° 42.9′	2055	*MAB 13812.2*
16	*E. triglochidiatus* subsp. *triglochidiatus*	Zia, Sandoval Co., NM	11	35° 39′ 106° 52′	1975	*MAB 13553,* 13553.1

Results

Principle Components Analysis (PCA)

Flower characters dominated the first two components of the PCA analysis that included all characters (Table 4). When components one and two were plotted together (not shown), however, there was a poor grouping of individuals within their respective taxa. Component three, which also explained a large percent of the total variance, had a stronger loading for stem characters. When components one and three were plotted together, individuals of the three taxa began to resolve but there remained a great deal of overlap (Fig. 2). For the PCA using only flower characters, none of the components adequately grouped individuals into species.

As with the interspecific analysis, stem characters discriminated individuals among taxa of *E. arizonicus* better than flower characters. A scatterplot of the first two components of PCA defined two groups that maintained the identity of individuals within populations (Fig. 3). One group was defined by populations one, two, and three, and the other group by populations four, five, and six. The first group contained the type locality for *E. arizonicus* subsp. *arizonicus* (population one) and the second for *E. arizonicus* subsp. *nigrihorridispinus* (population six). The highest loadings in the first component were for length of both central and radial spines, number of central spines, and stem diameter (Table 5). The highest loadings in the second component were for the distance between areole, thickness of central spine, and stem diameter.

Descriptive statistics, based on the defined populations, are presented in Table 6. Those for outgroups are presented in Table 7.

Unweighted Pair Group Method with Arithmetic Mean (UPGMA)

Results from a UPGMA analysis of stem characters for *Echinocereus arizonicus* with *E. triglochidiatus* subsp. *mojavensis* as an outgroup indicated that all populations were placed correctly within their respective taxa (Fig. 4). As expected, the outgroup (populations 11–14) was placed with the greatest phenetic distance with respect to populations within *E. arizonicus*. Populations of both *E. arizonicus* subsp. *arizonicus* (populations 1–3) and *E. arizonicus* subsp. *nigrihorridispinus* (populations 4–6) were distinctly grouped and the single population of *E. arizonicus* subsp. *matudae* (population 7) placed basally to either of the other two subspecies.

Multivariate Analysis of Variance (MANOVA)

Individuals of *E. arizonicus* subsp. *arizonicus*, as a group, possessed seven characters with distinct means: stem length, stem diameter,

Table 4. Component Loadings for all Characters of PCA with Varimax Rotation of Populations of *E. arizonicus* (Excluding *E. arizonicus* subsp. *matudae*), *E. santaritensis*, and *E. triglochidiatus*. For translation of character acronyms, see Table 1.

	Component				
	1	2	3	4	5
STYLEL	0.9	0.0	−0.1	0.0	0.0
FLRL	0.9	−0.2	0.0	−0.0	0.2
STAMENL	0.8	0.1	0.1	−0.1	−0.3
LTOUPPER	0.8	0.2	−0.1	−0.2	0.3
NRADIALS	0.0	0.9	0.0	−0.1	0.0
NCENTRALS	0.1	0.9	0.0	−0.1	−0.1
DBTWARLS	0.1	−0.8	0.1	0.3	−0.1
NRIBS	−0.0	0.8	0.0	0.1	0.3
OVARYL	0.4	−0.5	0.1	−0.1	0.3
NCTRYDIA	−0.1	0.0	0.9	−0.1	−0.1
OUTSDIA	0.0	0.1	0.8	0.1	0.1
STYLEDIA	0.0	−0.0	0.6	−0.0	0.0
LCENTRALS	−0.1	0.1	−0.0	0.9	−0.1
LRADIALS	−0.1	−0.4	−0.0	0.8	0.2
AXIALL	0.4	0.1	−0.2	−0.2	0.7
NTEPALS	0.0	0.0	0.3	0.3	0.6
STEMDIA	0.1	−0.1	0.2	−0.2	0.0
STEML	−0.1	0.3	0.1	0.1	0.2
THKNCNTR	−0.0	−0.1	0.2	0.2	−0.4
FLRWIDTH	0.5	−0.0	0.3	0.2	0.2
SPINEL	0.2	0.5	0.1	0.4	−0.0
		Percent of total variance explained			
	17.0	17.8	10.3	9.8	7.2

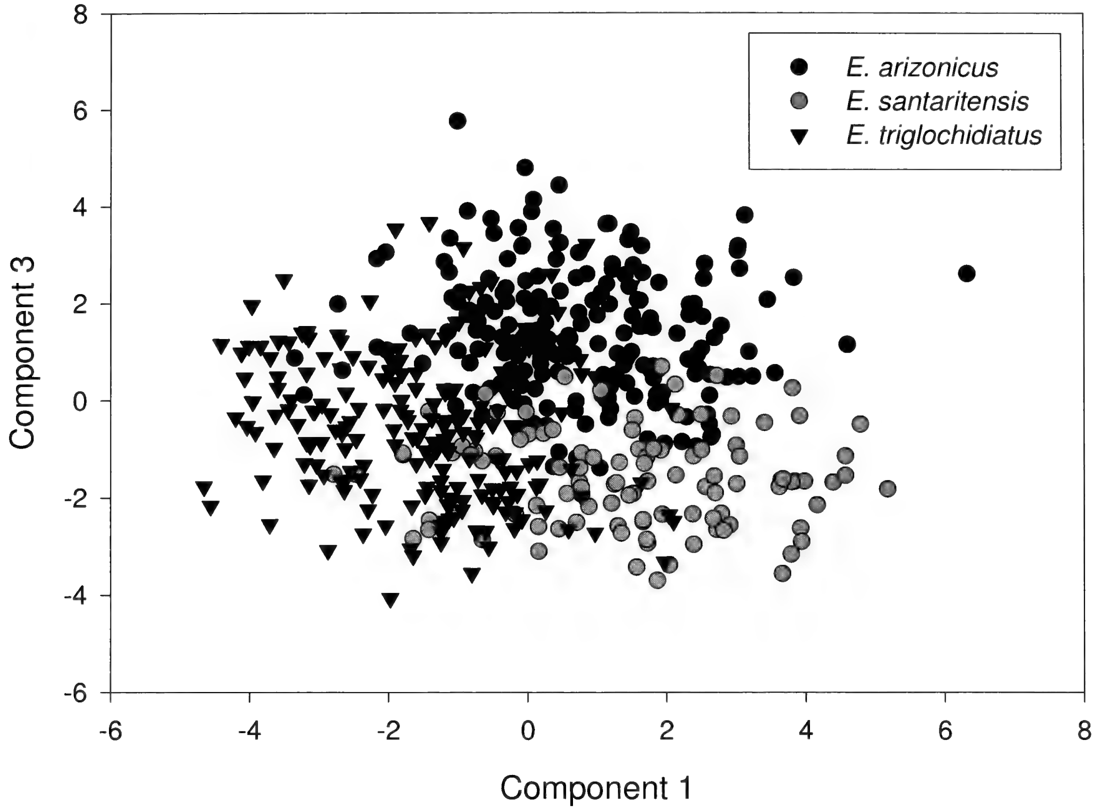

FIG. 2. Scatterplot of components 1 and 3 for PCA with varimax rotation using all characters for individuals of *E. arizonicus*, *E. santaritensis*, and *E. triglochidiatus*.

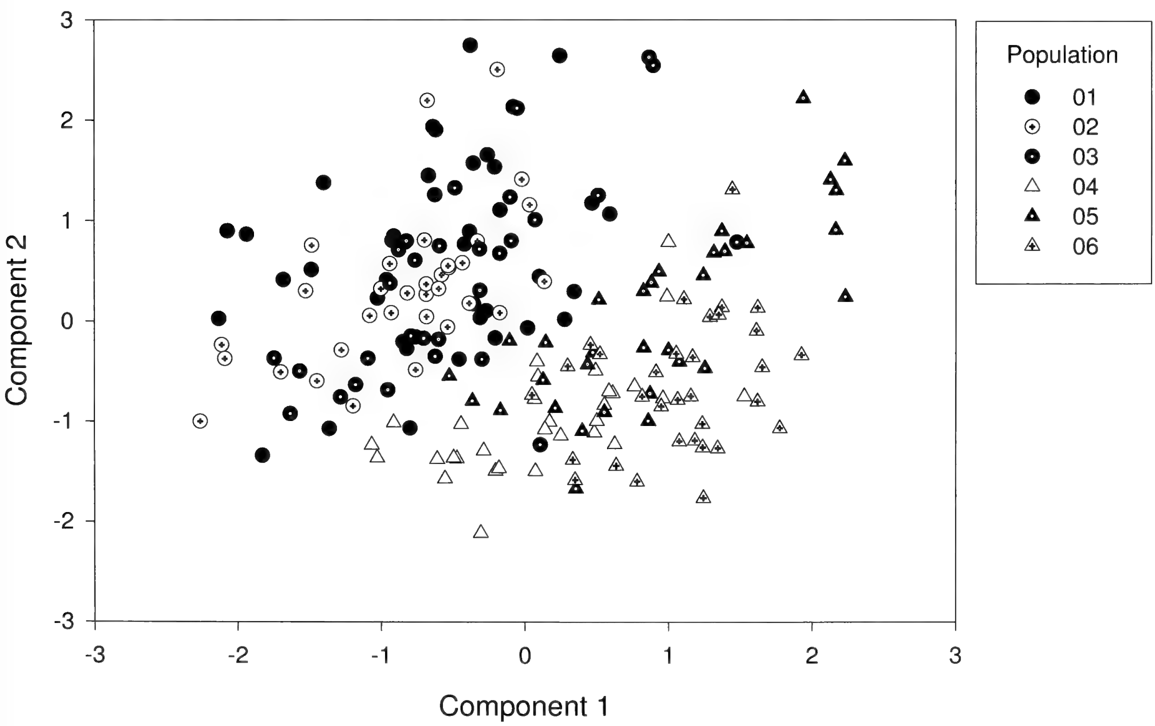

FIG. 3. Scatter plot of first two components of PCA with varimax rotation including stem characters for populations of *E. arizonicus*, excluding the one population of *E. arizonicus* ssp. *matudae*.

TABLE 5. COMPONENT LOADINGS FOR STEM CHARACTERS OF PCA WITH VARIMAX ROTATION OF POPULATIONS OF *E. ARIZONICUS*, EXCLUDING THAT OF *E. ARIZONICUS* SUBSP. *MATUDAE*.

	Component		
	1	2	3
NCENTRALS	0.8	−0.1	−0.1
LCENTRALS	0.8	−0.3	0.4
NRADIALS	0.8	0.0	0.0
LRADIALS	0.7	−0.3	0.4
DRIBS	0.6	−0.1	−0.3
STEML	−0.0	0.8	−0.2
STEMDIA	−0.4	0.8	0.2
DBTWARLS	0.0	0.7	0.5
THKNCNTR	−0.0	0.1	0.8
	Percent of total variance explained		
	30.7	20.7	16.6

distance between areoles, number of central spines, number of radial spines, length of pericarp, and style diameter (Table 8). Individuals of *E. arizonicus* subsp. *nigrihorridispinus*, as a group, possessed ten characters with distinct means: stem length, number of ribs, distance between areoles, number of centrals, number of radials, length of radials, flower length, pericarp spine length, style length, and ovary length (Table 8).

Discriminant Analysis

Discriminant analysis correctly classified 97.8% of the original grouped cases that included all of the study taxa (Table 9). Individuals of *E. arizonicus* subsp. *arizonicus* were classified correctly 97.0%, with 3.0% incorrectly classified as *E. arizonicus* subsp. *nigrihorridispinus*. Individuals of *E. arizonicus* subsp. *nigrihorridispinus* were correctly classified 94.7%, with 2.1% incorrectly classified as *E. arizonicus* subsp. *arizonicus* and 3.2% as *E. santaritensis*. A single individual (1%) of *E. santaritensis* was misclassified as *E. arizonicus* subsp. *nigrihorridispinus* and one as *E. triglochidiatus* subsp. *mojavensis*. Within *E. triglochidiatus*, only a single individual was misclassified, which was between the two subspecies. All between group correlations were highly significant (Table 10). The jackknifed classification matrix showed a one percent reduction in correct classification among each group.

DISCUSSION

Phenetic analysis presented herein supports the recognition of at least two infraspecific taxa within *E. arizonicus*: *E. arizonicus* subsp. *arizonicus* and *E. arizonicus* subsp. *nigrihorridispinus*. Although PCA shows incomplete interspecific resolution among the species sampled, there were significant differences in means for several morphological characters between *E. arizonicus* subsp. *arizonicus* and *E. arizonicus* subsp. *nigrihorridispinus*. Morphological differences coupled with allopatric geographic distribution have long been considered basic criteria for the recognition of two separate subspecies (Stebbins 1950; Lawrence 1951). Most of the known geographical distribution for *E. arizonicus* is represented by *E. arizonicus* subsp. *nigrihorridispinus*, which was the most variable subspecific taxon within the species in terms of the diagnostic stem characters. Individuals of *E. arizonicus* subsp. *arizonicus*, which have a limited geographic range, were more variable with respect to most flower characters.

Populations of *E. arizonicus* subsp. *arizonicus* differed significantly from those of *E. arizonicus* subsp. *nigrihorridispinus* in the means of most characters measured (Table 8). However, as shown by PCA, flower characters, as a group, were not generally diagnostic within the perfect-flowered taxa as a whole and no single flower character appeared to be useful in separating populations of *E. arizonicus* subsp. *arizonicus* from those of *E. arizonicus* subsp. *nigrihorridispinus*. Although stem characters were shown to be more diagnostic than flower characters, the former tend to be more affected by factors of age and environment. Stem diameter, for example, should be avoided as a key character because of its correlation with available water. Although age is generally a critical factor in stem length, stem length is mostly determinate within section *Triglochidiatus* because of its cespitose habit. In addition, the effects of age were minimized in the present study by the measurement of only mature individuals. Diagnostic characters that are less affected by age and environment are number of ribs, number and length of central spines, and number and length of radial spines. Although even these characters may be affected by etiolation, no individuals occurring in deep shade were included in the present study.

The geographic ranges, as defined herein, of *E. arizonicus* subsp. *arizonicus* and *E. arizonicus* subsp. *nigrihorridispinus* differs from that of Blum et al. (1998) in that populations of *E. arizonicus* subsp. *arizonicus* are more restricted.

Data herein were not sufficient to adequately evaluate the taxonomic circumscription of *E. arizonicus* subsp. *matudae*. Although individuals within the single known population possessed the fewest ribs, greatest distance between areoles, and fewest central and radial spines in comparison to those of the other two subspecies, additional populations of *E. arizonicus* subsp. *matudae*, should be sought and measured in order to properly address morphological variation throughout its range.

TABLE 6. DESCRIPTIVE STATISTICS OF *E. ARIZONICUS*.

Character	*E. arizonicus* subsp. *arizonicus*					*E. arizonicus* subsp. *nigrihorridispinus*					*E. arizonicus* subsp. *matudae*				
	N	Min	Max	0	SD	N	Min	Max	0	SD	N	Min	Max	0	SD
STEML	104	14	48	29.6	7.9	96	13	47	25.2	6.6	35	8.5	39.0	23.1	7.8
STEMDIA	104	5.7	10.3	8.1	1.0	96	3.7	8.8	6.1	0.9	35	5.6	9.7	7.8	1.0
NRIBS	104	7	11	8.8	0.6	96	8	12.7	9.6	0.7	35	6.0	8.3	7.1	0.5
DBTWARLS	104	9	18.7	13.6	2.3	96	6.7	18	11.5	2.4	35	11.7	27.7	20.1	3.4
NCENTRALS	104	1	5	2.9	0.9	96	2	6	4.0	0.7	35	0.7	3.0	1.6	0.7
NRADIALS	104	5	12.3	9.1	1.3	96	7.3	13	10.2	1.4	35	5.3	10.3	7.6	1.0
LRADIALS	104	9	24.7	12.4	2.5	96	9	31.3	18.7	4.7	35	13.7	29.7	20.9	4.2
LCENTRALS	104	15.3	58.3	26.0	7.2	96	21.3	59	40.5	8.8	35	21.0	52.3	31.6	6.0
THKNCNTR	104	0.62	1.37	0.95	0.15	96	0.53	1.53	0.88	0.18	35	0.59	1.67	1.04	0.19
FLRL	104	47	93.3	67.7	9.0	96	46.3	74.3	62.5	5.07	2	56.0	78.0	67.0	15.6
FLRWIDTH	104	33.3	54.3	42.4	4.6	96	30	55	40.9	5.4	2	39.0	43.7	41.4	3.3
OUTSDIA	104	8.7	16	12.0	1.6	96	9	17	11.8	1.4	2	16.0	16.0	16.0	0.0
AXIALL	104	3	29	12.8	5.2	96	2.7	16	7.5	3.6	2	4.0	6.0	5.0	1.4
LTOUPPER	104	25	58.3	39.5	6.2	96	26	46	37.4	4.1	2	30.0	49.0	39.5	13.4
NTEPALS	104	17	37	22.9	3.0	96	17	33	23.5	2.8	2	22.0	25.7	23.8	2.6
STYLEDIA	104	1.20	2.37	1.74	0.24	96	1.07	2.15	1.61	0.20	2	1.90	2.05	1.98	0.11
SPINEL	104	7	15.5	10.6	1.9	96	7	19	11.7	2.2	2	7.0	9.0	8.0	1.4
STYLEL	104	31.7	53.7	43.4	5.3	96	28.3	50.7	41.0	3.8	2	37.0	49.7	43.4	9.0
NCTRYDIA	104	2	7.5	3.6	1.1	96	2	6	3.3	0.6	2	4.0	4.0	4.0	0.0
OVARYL	104	3	11.3	7.2	1.8	96	2.5	12	5.8	2.0	2	4.0	8.3	6.2	3.0
STAMENL	104	27	50.3	39.5	5.4	96	26	47.3	37.8	4.3	2	32.0	42.0	37.0	7.1

TABLE 7. DESCRIPTIVE STATISTICS OF OUTGROUPS.

Character	*E. triglochidiatus* subsp. *mojavensis*					*E. triglochidiatus* subsp. *triglochidiatus*					*E. santaritensis*				
	N	Min	Max	0	SD	N	Min	Max	0	SD	N	Min	Max	0	SD
STEML	132	5.0	45.0	21.1	10.0	73	6.0	25.0	13.2	4.2	105	8.0	36.0	18.4	6.9
STEMDIA	132	4.8	9.0	6.1	0.9	73	5.0	9.0	6.4	1.0	105	4.0	7.0	5.4	0.7
NRIBS	132	7.7	13.0	9.0	0.7	73	5.0	8.5	6.8	0.6	105	8.0	12.0	9.8	0.8
DBTWARLS	132	7.7	25.7	16.4	4.3	73	14.0	36.7	22.8	5.6	105	6.0	14.0	9.4	1.7
NCENTRALS	132	0.0	2.0	1.0	0.4	73	0.0	1.0	0.4	0.4	105	1.0	5.0	3.5	0.7
NRADIALS	132	4.3	9.0	6.8	1.2	73	1.7	6.7	4.4	1.2	105	7.0	12.0	9.5	1.1
LRADIALS	132	13.0	62.7	31.0	10.3	73	0.8	37.7	22.0	6.2	105	7.7	34.3	16.5	4.9
LCENTRALS	130	18.3	83.7	40.9	12.3	42	14.3	58.3	29.1	9.2	105	17.7	49.0	31.3	8.3
THKNCNTR	130	0.3	1.2	0.7	0.2	47	.40	1.74	0.91	0.26	105	0.33	1.05	0.60	0.16
FLRL	132	48.5	88.3	65.6	7.3	73	54.7	87.0	70.4	6.7	105	47.0	115.5	67.5	9.0
FLRWIDTH	132	32.0	60.7	40.7	6.2	73	33.0	50.7	41.8	4.4	105	32.0	56.7	42.1	5.5
OUTSDIA	132	7.0	14.7	10.9	1.7	73	8.0	13.7	10.6	1.1	105	7.3	12.7	9.8	1.1
AXIALL	132	3.0	23.0	12.0	4.6	73	3.0	20.0	6.8	3.4	105	8.0	31.5	13.6	3.2
LTOUPPER	132	22.7	55.0	37.0	5.5	72	27.5	53.0	37.2	4.7	105	31.0	71.5	44.7	6.6
NTEPALS	132	16.3	32.5	24.0	3.1	73	15.7	29.0	22.4	2.7	105	16.5	27.5	22.7	2.0
STYLEDIA	132	1.10	2.10	1.53	0.21	73	1.15	2.01	1.59	0.18	105	1.10	1.90	1.47	0.18
SPINEL	132	6.3	16.7	9.9	1.9	73	5.0	15.0	8.4	2.3	105	6.7	16.7	10.5	1.7
STYLEL	132	26.5	53.3	42.8	5.2	73	37.0	56.7	46.0	4.2	105	27.5	69.0	48.6	6.5
NCTRYDIA	132	1.7	5.7	3.1	0.8	73	2.0	5.7	3.2	0.7	105	1.8	5.5	3.1	0.7
OVARYL	132	3.5	16.3	7.6	2.0	73	4.3	13.7	8.9	2.2	105	3.7	17.5	6.6	1.9
STAMENL	132	26.5	50.7	35.5	3.8	73	32.5	52.0	40.1	4.1	105	21.0	56.5	38.2	6.9

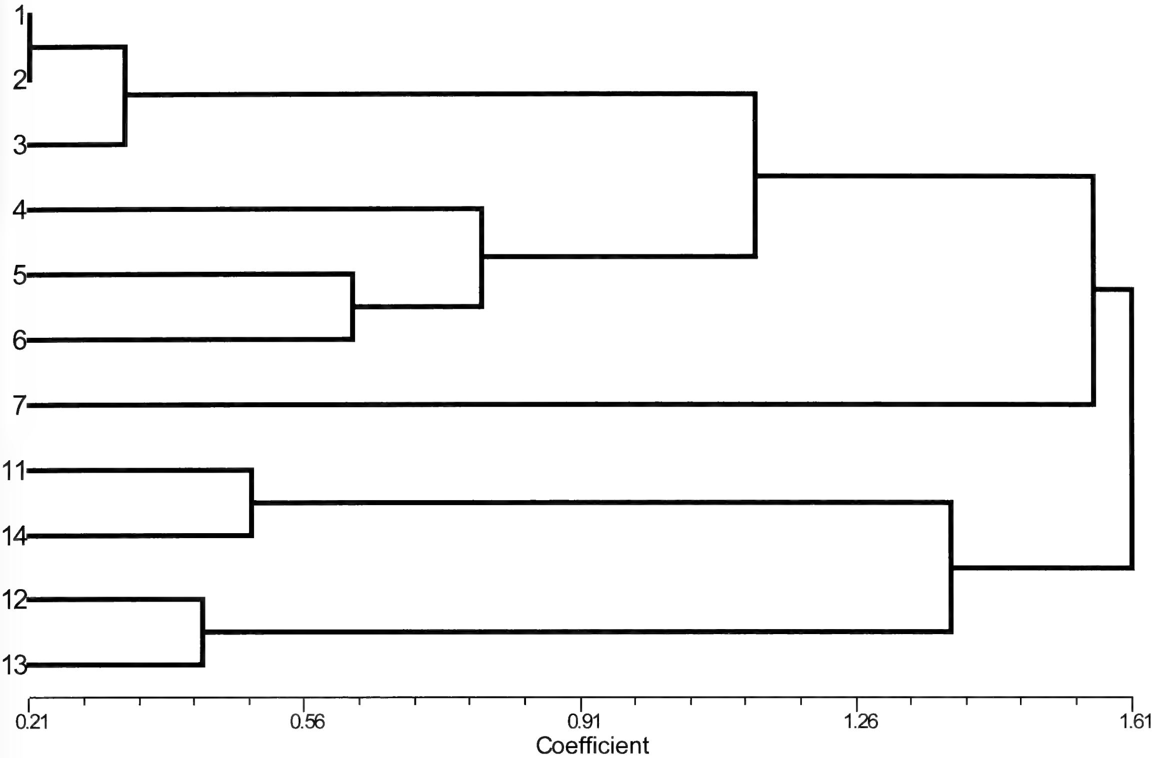

FIG. 4. Phenogram from UPGMA including populations of *E. arizonicus* and *E. triglochidiatus* ssp. *mojavensis*. Matrix composed of mean values for each character.

Similarly, data were not adequate for the assessment of the taxonomic circumscription of the two subspecies of *E. triglochidiatus*, primarily because of the lack of data from the type locality for *E. triglochidiatus* ssp. *triglochidiatus*. Furthermore, UPGMA suggests that *E. triglochidiatus* subsp. *mojavensis* may be composed of more than one taxonomically definable group, a western

TABLE 8. SELECTED HOMOGENEOUS SUBSETS FROM MANOVA SIGNIFICANCE (DUNCANS MULTIPLE RANGE TEST) WHERE $P > 0.02$.; SUBSET A HAS THE SMALLEST MEAN VALUE AND E HAS THE LARGEST. For all subsets containing a single taxon, $p = 1.000$. 1 = *E. arizonicus* subsp. *arizonicus*, 2 = *E. arizonicus* subsp. *nigrihorridispinus*, 3 = *E. santaritensis*, 4 = *E. triglochidiatus* subsp. *mojavensis*, 5 = *E. triglochidiatus* subsp. *triglochidiatus*. See Tables 5 and 6 for specific means.

	Subset				
	A	B	C	D	E
STEML	5	3	4	2	1
STEMDIA	3	4, 2	2, 5	1	
NRIBS	5	1, 4	2	3	
DBTWARLS	3	2	1	4	5
NCENTRALS	5	4	1	3	2
NRADIALS	5	4	1	3	2
LRADIALS	1	3	2	5	4
LCENTRALS	1	5, 3	4, 2		
THKNCNTR	3	4	2, 5	5, 1	
FLRL	2	4, 3, 1	5		
OUTSDIA	3	5, 4	2, 1		
LTOUPPER	4, 5, 2	1	3		
STYLEDIA	3, 4	5, 2	1		
SPINEL	5	4	3, 1	2	
STYLEL	2	4, 1	5	3	
OVARYL	2	3	1, 4	5	
STAMENL	4	2, 3	1, 5		

TABLE 9. PREDICTED GROUP MEMBERSHIP FOR DA AMONG INDIVIDUALS WITHIN POPULATIONS PRECLASSIFIED AS *E. ARIZONICUS* SUBSP. *ARIZONICUS*, *E. ARIZONICUS* SUBSP. *NIGRIHORRIDISPINUS*, *E. SANTARITENSIS*, *E. TRIGLOCHIDIATUS* SUBSP. *MOJAVENSIS*, AND *E. TRIGLOCHIDIATUS* SUBSP. *MOJAVENSIS*. 97.8% of original grouped cases were correctly classified.

Taxon	*E. arizonicus* subsp. *arizonicus*	*E. arizonicus* subsp. *nigrihorridispinus*	*E. santaritensis*	*E. triglochidiatus* subsp. *mojavensis*	*E. triglochidiatus* subsp. *triglochidiatus*	Total
		By number of individuals				
E. arizonicus subsp. *arizonicus*	98	3	0	0	0	101
E. arizonicus subsp. *nigrihorridispinus*	2	90	3	0	0	95
E. santaritensis	0	1	102	1	0	104
E. triglochidiatus subsp. *mojavensis*				128	1	129
E. triglochidiatus subsp. *triglochidiatus*	0	0	0	0	72	72
		By percent of individuals				
E. arizonicus subsp. *arizonicus*	**97.0**	3.0	.0	.0	.0	100
E. arizonicus subsp. *nigrihorridispinus*	2.1	**94.7**	3.2	.0	.0	100
E. santaritensis	.0	1.0	**98.1**	1.0	.0	100
E. triglochidiatus subsp. *mojavensis*	.0	.0	.0	**99.2**	.8	100
E. triglochidiatus subsp. *triglochidiatus*	.0	.0	.0	.0	**100.0**	100

group represented by the type and an eastern group, perhaps represented by the basionym *Cereus mojavensis* Engelm. & J. M. Bigelow var. *zuniensis* J. M. Bigelow & Engelm, for which the type locality is in Canyon Diablo, east of Flagstaff, Arizona.

Evidence from comparative morphology and geographic distribution suggests that tetraploid populations within section *Triglochidiatus*, specifically *E. santaritensis*, probably arose from *E. arizonicus* subsp. *nigrihorridispinus*. The two taxa are morphologically similar, sympatric over much of their ranges, and are both perfect-flowered.

KEY TO THE SUBSPECIES OF *ECHINOCEREUS ARIZONICUS*

Note that populations display a high degree of morphological variability among individuals and, consequently, data from several individuals should be averaged for identification. *Echinocereus arizonicus* subsp. *matudae* is included in a somewhat preliminary sense in that additional data may be needed to address morphological variation throughout its range.

A- Stems of mature individuals with mostly 10 ribs, central spines averaging 4 in number and mostly 4 cm long or longer, radial spines

TABLE 10. BETWEEN GROUPS F-MATRIX (DF = 21, 701). $P < 0.01$ FOR ALL VALUES. Wilks' Lambda = 0.004, Approx. $F = 70.2$ prob < 0.00001.

Taxon	*E. arizonicus* subsp. *arizonicus*	*E. arizonicus* subsp. *nigrihorridispinus*	*E. santaritensis*	*E. triglochidiatus* subsp. *mojavensis*	*E. triglochidiatus* subsp. *triglochidiatus*
E. arizonicus subsp. *arizonicus*	0.0				
E. arizonicus subsp. *nigrihorridispinus*	36.3	0.0			
E. santaritensis	81.7	36.1	0.0		
E. triglochidiatus subsp. *mojavensis*	118.3	97.1	75.6	0.0	
E. triglochidiatus subsp. *triglochidiatus*	115.0	144.0	153.7	79.6	0.0

averaging 10 in number. Arizona: Cochise, Graham, Greenlee, Pima, and Santa Cruz Counties; New Mexico: Hidalgo and Luna counties; Mexico: probable occurrence in Sonora and Chihuahua . . . . *E. arizonicus* subsp. *nigrihorridispinus*

AA- Stems of mature individuals with mostly 9 or fewer ribs, central spines averaging 3 or fewer in number and mostly shorter than ca. 3 cm, radial spines averaging 9 or fewer in number . . B

B- Stems of mature individuals with mostly 9 ribs, central spines averaging 3 in number, radial spines averaging 9 in number and mostly shorter than 1.3 cm. Arizona: NE Pinal and SW Gila Counties . . . . *E. arizonicus* subsp. *arizonicus*

BB- Stems of mature individuals with mostly 7 ribs, central spines averaging fewer than 2 in number, radial spines averaging fewer than 8 in number and mostly longer than 2 cm. Mexico: Chihuahua. . . . . *E. arizonicus* subsp. *matudae*

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CONTRIBUTIONS TOWARD A BRYOFLORA OF NEVADA: BRYOPHYTES NEW FOR THE SILVER STATE, PART II

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ABSTRACT

Two hornworts, five liverworts, and 24 mosses are reported new for the state of Nevada. The phylum Anthocerotophyta as represented by the families Anthocerotaceae and Notothyladaceae, the liverwort families Antheliaceae, Cleveaceae, Fossombroniaceae, and Pseudolepicoleaceae, and the moss family Bruchiaceae are all new for the state. Genera new for Nevada include: *Anthelia*, *Anthoceros*, *Athalamia*, *Blepharostoma*, *Bruchia*, *Codriophorus*, *Conostomum*, *Ditrichum*, *Fossombronia*, *Gemmabryum*, *Phaeoceros*, *Ptychostomum*, and *Rosulabryum*. A new treatment of the widespread *Bryum caespiticium* Hedwig is adopted for North America, with the segregates *Bryum badium* (Bridel) W. P. Schimper and *Bryum kunzei* Hornschuch reported for the first time for North America.

Key Words: bryophytes, hornworts, liverworts, mosses, new records, bryogeography, Nevada.

This is the second installment in our ongoing study to document bryophytes (hornworts, liverworts and mosses) as new for the state of Nevada based on examination of specimens. An overview of the project and a map of Nevada are provided in Shevock et al. (2005). In this installment, we have focused on the review of Nevada specimens within the families Bryaceae and Leskeaceae. These families are currently being studied by the first author for treatments in the forthcoming bryophyte volumes of the Flora North America Project (BFNA). The genus *Bryum* s.l. is projected to be the largest genus of mosses in Nevada, currently represented by 26 species. Additional *Bryum* s.l. species are expected to be documented for Nevada with continued collection, and several species new to science, which will be published elsewhere, are also known from the state.

Bryum s.l. is a large (~500 species) worldwide genus that as traditionally described is polyphyletic. For the upcoming BFNA, *Bryum* Hedwig and related species will be segregated into a series of smaller more natural genera, based primarily on gametophyte characters, although some sporophyte characters are also important. The following genera are treated here: *Bryum* s.s., *Gemmabryum* Spence & Ramsay, *Ptychostomum* Hornschuch, and *Rosulabryum* Spence (Spence 1996, 2005; Spence & Ramsay 2005). Two segregates out of the *Bryum caespiticium* Hedwig complex, *B. badium* and *B. kunzei*, are accepted here for the first time and are thus new for North America. Previous work documented 13 species of *Bryum* s.l. from Nevada (Lawton 1958).

During the 2005 field season, two hornworts were documented for Nevada. Prior to these collections, hornworts were presumed to be absent from the state due to a perception of a lack of suitable habitat. For these collections, we have followed the hornwort classification and nomenclature as proposed by Stotler & Crandall-Stotler (2005). Finding hornworts for the first time in Nevada indicates how much collection work remains to be done to complete basic inventories of biological diversity.

HORNWORTS [ANTHOCEROPHYTA]

***Anthoceros fusiformis* Austin** [Anthoceroceae]

Humboldt Co.: BLM Winnemucca District, Pine Forest Range, below Blue Lakes, 6 Aug 2005, *Shevock & Nachlinger 27531* (CAS, MO, NY, SIU, UC, UNLV, WTU) [determined by Bill Doyle]. On moist granitic soil along bank of stream in a meadow stringer. At nearly 8000 ft, we believe this occurrence is among the highest elevation documented for a hornwort in western North America.

Phaeoceros carolinianus **(Michaux) Proskauer** [Notothyladaceae]

Clark Co.: BLM Red Rock Canyon National Conservation Area. Pine Creek, 4 Apr 2005, *Brinda 69* (CAS, UNLV). On seep of stream bank. This material was examined by Bill Doyle and provisionally assigned to this species because the collection lacks mature spores. However, we feel fairly confident that this is indeed this species since *P. carolinianus* was recently discovered from another locality in the Mojave Desert within Death Valley National Park (Laeger 2005). No other *Phaeoceros* is documented from the Mojave Desert.

LIVERWORTS [MARCHANTIOPHYTA]

Anthelia juratzkana **(Limpricht) Trevis** [Antheliaceae]

Elko Co.: Humboldt National Forest, East Humboldt Mts., East Humboldt Wilderness, cirque above Smith Lake, 29 Jul 2004, *Shevock 25982* (CAS, MO, NY, SIU, UC, UNLV) [determined by Bill Doyle]. On moist soil at base of boulders.

Athalamia hyalina **(Sommerfelt) S. Hattori** [Cleveaceae]

Elko Co., Humboldt National Forest, Ruby Mts., Lamoille Canyon Scenic Area, Ruby Crest National Recreation Trail (043) between Liberty Pass and Lamoille Lake, 31 Jul 2004, *Shevock 26049* (CAS, UC, UNLV) and trail to Dollar Lakes, 20 Jul 2002, *Shevock & Glazer 22501* (CAS, UNLV) [determined by Bill Doyle]. On moist soil of intermittent rivulet from snowmelt.

Blepharostoma trichophyllum **(Linneaus) Dumortier** [Pseudolepicoleaceae]

Elko Co.: Humboldt National Forest, Jarbidge Mts., Jarbidge Wilderness, Forest Trail 106 about 1 mi below Jarbidge Lake, 6 Aug 2004, *Shevock, Glazer, & Howell 26129* (CAS, MO, UNLV) [determined by Bill Doyle]. On wet and shaded underhang bank of streamlet.

Fossombronia **sp.** [Fossombroniaceae]

Note: Since this specimen lacks sporophytes, naming it to the species level is problematic. Nonetheless, this plant is without doubt a *Fossombronia* which is a genus new for the Nevada bryoflora.

Elko Co.: Humboldt National Forest, East Humboldt Mts., East Humboldt Wilderness, cirque above Smith Lake, 29 Jul 2004, *Shevock 25984a* (CAS) [confirmed by Bill Doyle]. On moist soil wet from snowmelt.

Mannia californica **(Gottsche) Wheeler** [Aytoniaceae]

Clark Co.: Spring Mts., BLM Red Rock Canyon National Conservation Area, White Rock Spring, 25 Mar 2005, *Stark & Brinda s.n.* (CAS, UNLV) [confirmed by Alan Whittemore] and Pine Creek Canyon, 4 Apr 2005, *Shevock, Brinda, & Stark 26523* (CAS, UNLV); **Lincoln Co**: South Pahroc Range, south side of Pahroc Summit along highway 93, 3 Apr 2005, *Shevock & Brinda 26494* (CAS, UNLV) [confirmed by Bill Doyle]. On soil at base of rock outcrops and ledges in partial shade.

MOSSES [BRYOPHYTA]

Bruchia bolanderi **Lesquereux** [Bruchiaceae]

Washoe Co.: Toiyabe National Forest, Carson Range, Sierra Nevada, Tahoe Meadows along Ophir Creek, 28 Jul 2004, *Shevock 25973* (CAS, MO, UC, UNLV) and 29 Aug 2004, *Shevock, Ertter, & Matson 26165* (CAS, KRAM, MO, NY, UBC, UNLV). On moist vertical clay walls of creek bank and on moist exposed soil in fen habitats.

Bryum badium **(Bridel) W. P. Schimper** [Bryaceae]—see *Ptychostomum badium*

Bryum bimum **(Schreber) Turner** [Bryaceae]—see *Ptychostomum bimum*

Bryum elegans Nees [Bryaceae]—see *Rosulabryum elegans*

Bryum flaccidum **Bridel** [Bryaceae]

Clark Co.: Toiyabe National Forest, Spring Mts., Kyle Canyon at Mary Jane Falls Trailhead, 19 Jun 1996, *Stark 1359* (UNLV); **Douglas Co.**: Pine Nut Mts., canyon about 1 mi north of Jack Wright Summit off highway 208, 2 May 2003, *Shevock & Durham 24042* (CAS, UNLV); **Elko Co.**: Humboldt National Forest, Jarbidge Mts., along Pine Creek near junction with Jarbidge River about 4 mi south of town of Jarbidge, 26 Aug 2002, *Shevock & Glazer 22795* (CAS, UNLV); Humboldt National Forest, Ruby Mts., Harrison Pass Road above Harrison Pass Creek, 30 Jul 2004, *Shevock 26029* (CAS, MO, NY, UNLV). On rock walls. Note: this species is a *Rosulabyrum* and will be transferred at a future date.

Bryum gemmiparum **De Notaris** [Bryaceae]

Clark Co.: Red Rock Canyon National Conservation Area, Spring Mts., Lower Pine Creek, 25 Mar 2000, *Spence 5421* (CAS, UNLV).

Bryum kunzei **Hornschuch** [Bryaceae]

Clark Co.: Toiyabe National Forest, Spring Mts., south end of Bristlecone Trail near ski lift, 12 Jun 1996, *Stark 1275* (UNLV) and Foxtail Canyon near Sponge Springs, 27 Jun 1996, *Stark 1414* (UNLV); **Elko Co.**: Humboldt National Forest, Ruby Mts., Harrison Pass Road above Harrison Pass Creek, 30 Jul 2004, *Shevock 26027* (CAS, MO, NY, UNLV, WTU); **Eureka Co.**: Roberts Mts., Jackass Creek, 10 Jun 2003, *Nachlinger & Tiehm 2435* (CAS, MO, NY, UNLV, WTU); **Lander Co.**: Toquima Range, Toiyabe National Forest, Toquima Caves, 16 mi east of highway 376, 30 May 2002, *Shevock & Glazer 22361* (CAS, MO, NY, UNLV); **Nye Co.**: Grant Range, Scofield Canyon at east side of range, 4 Jul 2003, *Nachlinger & Taylor 2548* (CAS, MO, NY, UNLV); **White Pine Co.**: Kern Mts., south of Moffit Flat and west of Blue Mass, 13 Sep 2002, *Nachlinger & Provencher 2456a*

(CAS, MO, NY, UNLV). On compacted soil. New for North America. Note: this species is a *Ptychostomum* and will be transferred at a future date.

Bryum laevifilum **Syed** [Bryaceae]—see *Rosulabryum laevifilum*

Bryum lonchocaulon **C. Müller Hal.** [Bryaceae]—see *Ptychostomum lonchocaulon*

Bryum neodamense **Itzigsohn *in* C. Müller Hal.** [Bryaceae]—see *Ptychostomum neodamense*

Bryum radiculosum **Bridel** [Bryaceae]—see *Gemmabryum radiculosum*

Bryum subapiculatum **Hampe** [Bryaceae]—see *Gemmabryum subapiculatum*

Bryum tenuisetum **Limpricht** [Bryaceae]—see *Gemmabryum tenuisetum*

Bryum valparaisense **Thériot** [Bryaceae]

Clark Co.: Toiyabe National Forest, Spring Mts., Spring Hill north of Charleston Peak Resort, 7 Jun 1939, *Alexander 736* (UC). Note: this species is a *Gemmabryum* and will be transferred at a future date. Previous reports of *Bryum pyriferum* Crundwell & Whitehouse in North America can be referred to this species, which is Neotropical in distribution (Arts et al. 1995).

Codriophorus acicularis **(Hedwig) Bednarek-Ochyra & Ochyra** [Grimmiaceae]

Washoe Co.: Toiyabe National Forest, Carson Range, Sierra Nevada, Tahoe Meadows above Ophir Creek, 29 Aug 2004, *Shevock, Ertter, & Matson 26158a* (CAS, KRAM, UNLV) [determined by Dan Norris; confirmed by Halina Bednarek-Ochyra]. On rocks in channel of intermittent streamlet inundated during snowmelt. Note: The genus *Codriophorus* is one of three segregate genera recently separated from *Racomitrium* (Ochyra et al. 2003).

Codriophorus depressus **(Lesquereux) Bednarek-Ochyra & Ochyra** [Grimmiaceae]

Washoe Co.: Carson Range, Sierra Nevada, Lake Tahoe Basin Management Unit, 1.5 km north of Sand Harbor, 30 Apr 1980, *Lavin s.n.* (WTU) [determined by Halina Bednarek-Ochyra]. Note: This collection was the basis for *Racomitrium heterostichum*, a species newly reported for Nevada by (Lavin 1982). *Racomitrium heterostichum* can now be excluded from the Nevada bryoflora.

Conostomum tetragonum **(Hedwig) Lindberg** [Bartramiaceae]

Elko Co.: Humboldt National Forest, East Humboldt Mts., cirque above Smith Lake, 29 Jul 2004, *Shevock 25978* (CAS, MO, UC, UNLV); Humboldt National Forest, Ruby Mts., Ruby Mountains Wilderness, between Lamoille Lake and Liberty Pass, 31 Jul 2004, *Shevock 26048* (CAS, UNLV). Moist bare soil along rivulets and at base of boulders in alpine habitats.

Ditrichum flexicaule **(Schwägrichen) Hampe** [Ditrichaceae]

Elko Co.: Humboldt National Forest, Jarbidge Mts., Jarbidge River above Pine Creek Campground, 25 Aug 2002, *Shevock & Glazer 22758* (CAS, MO, NY, UBC, UC, UNLV, WTU) [determined by Bruce Allen]. On rock wall.

Fontinalis gigantea Sullivant [Fontinalaceae]

Elko Co.: East Ruby Mts., Humboldt National Forest, Lizzies Basin below Hole in the Wall Mtn., Leach Creek, 30 Jul 2004, *Shevock 26004* (CAS, KRAM, MO, NY, UBC, UC, WTU) [determined by Bruce Allen]. Attached to rocks and submerged in creek at lake outlet.

Gemmabryum radiculosum **(Bridel) J.R. Spence & H.P. Ramsay** [Bryaceae]

Nye Co.: Nevada Test Site, Frenchman Flat, Feb 2005, *Brinda 128* (CAS, UNLV). On sandy soil.

Gemmabryum subapiculatum **(Hampe) J.R. Spence & H.P. Ramsay** [Bryaceae]

White Pine Co.: Humboldt National Forest, Snake Range, Lower Hendry's Creek, southeast of Mt. Moriah, 20 Sep 2002, *Nachlinger & Provencher 2460* (CAS, MO, NY, UNLV).

Gemmabryum tenuisetum **(Limpricht) J.R. Spence & H.P. Ramsay** [Bryaceae]

Clark Co.: Virgin Mts., Lower Cabin Canyon, 15 Nov 2002, *Shevock, Glazer, Spence, & Nelson 23641* CAS, UNLV).

Grimmia hamulosa **Lesquereux** [Grimmiaceae]

Elko Co.: Humboldt National Forest, Jarbidge Mts., Jarbidge River near Buster Campground, 25 Aug 2002, *Shevock & Glazer 22736* (CAS, MA, MO, NY, UC, UNLV). **Washoe Co.**: Toiyabe National Forest, Carson Range, northern Sierra Nevada, slopes above Ophir Creek near Upper Price Lake, 29 Aug 2004, *Shevock & Matson 26162* (CAS, UNLV). On rock slabs, and sheet drainage areas seasonally moist generally from snowmelt.

Lescuraea saviana **(De Notaris) E. Lawton** [Leskeaceae]

Elko Co.: Humboldt National Forest, Ruby Mts., Harrison Pass Road above Harrison Pass Creek, 30 Jul 2004, *Shevock 26022* (CAS, MO, NY, UNLV).

Lescuraea saxicola **(W. P. Schimper *in* Bruch & W. P. Schimper) Molendo *in* Lorentz** [Leskeaceae]

White Pine Co.: Great Basin National Park, Snake Range, cliffs above Teresa Lake on trail to Wheeler Peak, 2 Oct 1984, *Norris 72391* (CAS, UC) [determined by Dan Norris; confirmed by John Spence]. On rock walls and boulders.

Pohlia obtusifolia **(Bridel) L. Koch** [Mniaceae]

Elko Co.: Humboldt National Forest, Ruby Mts., Lamoille Canyon Scenic Area, Ruby Crest National Recreation Trail (043) between Liberty Pass and Lamoille Lake, 31 Jul 2004, *Shevock 26053* (CAS, DUKE, UNLV) [determined by Jon Shaw]. On moist soil and gravels along intermittent rivulet from snowmelt.

***Ptychostomum badium* (Bridel) J. R. Spence** [Bryaceae]

White Pine Co.: Kern Mts., northwest side and south of Moffit Flat west of Blue Mass, 13 Sep 2002, *Nachlinger & Provencher 2456b* (CAS, UNLV). New for North America.

***Ptychostomum bimum* (Schreber) J. R. Spence** [Bryaceae]

Lander Co.: Toiyabe Range, Toiyabe National Forest, along forest road 002, 3.5 mi above Kingston Guard Station, 30 May 2002, *Shevock & Glazer 22346* (CAS, MO, NY, UNLV); **Nye Co.**: Quinn Canyon Range, Little Cherry Creek about 2 mi northwest of Adaven, 3 Jul 2003, *Nachlinger & Taylor 2545* (CAS, NY, UNLV).

***Ptychostomum lonchocaulon* (C. Müller Hal.) J. R. Spence** [Bryaceae]

Clark Co.: Toiyabe National Forest, Spring Mts., Kyle Canyon at Big Falls Trail, 19 Jun 1996, *Stark 1387 & 1388* (UNLV); **Elko Co.**: Knoll Mtn., Hice Spring, 11 Jun 2003, *Nachlinger & Tiehm 2537* (CAS, UNLV); **White Pine Co.**: Humboldt National Forest, Snake Range, Upper Hendry's Creek southeast of Mt. Moriah, 22 Sep 2002, *Nachlinger & Provencher 2463* (CAS, NY, UNLV).

***Ptychostomum neodamense* (Itzigsohn *in* C. Müller Hal.) J. R. Spence** [Bryaceae]

Clark Co.: Red Rock Canyon National Conservation Area, Spring Mts., First Creek, 26 Mar 2000, *Mancuso 2047* (UNLV).

***Racomitrium aciculare* Hedwig** [Grimmiaceae]—see *Codriophorus acicularis*

***Racomitrium depressum* Lesquereux** [Grimmiaceae]—see *Codriophorus depressus*

***Rosulabryum elegans* (Nees *in* Bridel) Ochyra** [Bryaceae]

Nye Co.: Phinney Canyon NE of Wahguyhe Peak, Grapevine Mts., Death Valley National Park, 18 Jan 2003, *Shevock, York, & Davis 23702* (CAS, UNLV). On rock in dry stream channel.

***Rosulabryum laevifilum* (Syed) Ochyra** [Bryaceae]

Elko Co.: Humboldt National Forest, Jarbidge Mts., Jarbidge Wilderness, Forest Trail 106 along Jarbidge River near junction of trail to Jarbidge Lake and Marys River, 6 Aug 2004, *Shevock, Glazer, & Howell 26146* (CAS, MO, NY, UNLV, WTU); **Nye Co.**: Death Valley National Park, Grapevine Mts., above Strozzi Ranch Site north of Wahguyhe Peak, 11 Jan 2002, *Shevock & York 21694* (CAS, UNLV). On soil and litter.

***Tortula guepinii* (Bruch & W. P. Schimper) Brotherus** [Pottiaceae]

Clark Co.: Eldorado Mts., Keyhole Canyon Archeological Site, north base of Keyhole Canyon, 8 Apr 1994, *Stark 205* (UNLV) [determined by Richard Zander]; Lake Mead National Recreation Area, Newberry Mts., Pipe Spring Canyon, vicinity of Pipe Spring, 4 Feb 1994, *Stark 98b* (UNLV). On crevice of north-facing boulders.

Acknowledgments

We acknowledge the continued contributions of several Nevada botanists and plant enthusiasts who have kindly supplied us with specimens for this ongoing inventory work. Special thanks to Bill Doyle and Alan Whittemore for providing determinations for our Nevada hornwort and liverwort collections. We also greatly appreciate the assistance by Bruce Allen, Jon Shaw, and Richard Zander for moss specimen determinations. John Hunter and two anonymous reviewers provided constructive comments that improved the final manuscript. Finally, we thank the various public land management agencies across the state of Nevada who continue to support this inventory by granting us botanical and research collecting permits. This research was funded in part by a Clark County (NV) Multiple Species Habitat Conservation Plan grant to UNLV and a National Geographic Society grant No. 5429-95 to LRS administered through the Missouri Botanical Garden.

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A NEW SPECIES OF *HESPEROLINON* (LINACEAE) FROM HUNTING CREEK IN NAPA COUNTY, CALIFORNIA

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ABSTRACT

A new species of *Hesperolinon* is described that is distinguished by its morphology, particularly its three carpels and styles, dichasial inflorescence, and certain petal characteristics. It is a serpentine endemic and may be related to *Hesperolinon bicarpellatum*.

Key Words: *Hesperolinon*, serpentine endemism, new species, Helen Sharsmith.

SPECIES TREATMENT

Hesperolinon sharsmithiae Richard O'Donnell, sp. nov.—TYPE: USA, California, Napa Co., serpentine chaparral about 180 m northwest of the junction of Cedar Creek and Hunting Creek, Paradise Valley, Napa County, California. About 122°24′W 38°47′N, about 270 m elevation. *Richard O'Donnell s.n.* (Holotype: JEPS). Collected 6-9-2005.

Hesperolinon sharsmithiae, sp. nov. Herba annua, 5–50 cm alta; Inflorescentia paniculata cymulis plerumque dichasialibus ramis secundariis opposites; Sepalis binis exterioribus et ternis interioribus minoribus vex porrectis; Petalis 3–4.5 mm longis, 2–2.5 mm latis, luteis; Filamentis 1.5–2.5 mm longis, antheris 1–1.5 mm longis; Ovario 3 – carpellato, stylis 3, 2–3.5 mm longis.

Annual; *Stem* 5–50 cm tall; *Leaves* linear, narrow at base, 15–20 mm long, 1–1.5 mm wide, stipular glands present; *Inflorescence* dichasial cyme, primary branches alternate, spreading, secondary branches equal and opposite, dichotomous; *Flowers* scattered, the ultimate branchlets bearing 1 or 2 flowers; *Pedicels* 0.5–2 mm long near tips of branches, 4–5 mm long on lower axils; *Sepals* 5, equal, sparsely glandular on margins, 3 mm long, oblanceolate, the two outer sepals and three inner sepals, connivent in bud; *Petals* oblanceolate to obovate, almost oval, erose, 3–4.5 mm long, 2–2.5 mm wide, yellow, sometimes red along midvein or elsewhere, attached to the rim of the cup; *Cup* yellow; *Stamens* yellow, filaments 1.5–2.5 mm long, each filament is continuous with the rim of the cup and at its base, each filament has a pair of short, narrow lobes on either side; anthers, yellow, 1–1.5 mm long, pollen grains yellow; *Ovary* 3-carpellate, ovules 6, styles 3, 2–3.5 mm long; *Fruit* globose capsule about 2 mm long and as wide.

Hesperolinon sharsmithiae is abundant in the serpentine chaparral along Hunting Creek in Napa County and the Sargent cypress forest on the bluffs above Hunting Creek in Lake County. This area is in the southern Inner North Coast Range. At the type locality, *H. sharsmithiae* is associated with *Cupressus sargentii* Jepson, *Arctostaphylos viscida* C. Parry, *Quercus durata* Jepson, *Streptanthus breweri hesperidis* (Jepson) Jepson, *Streptanthus glandulosus* Hooker, *Navarretia jepsonii* Jepson, *Vulpia microstachys* (Nutt.) Bent., *Cryptantha hispidula* Brand, *Allium fimbriatum* S. Watson, and *Allium falcifolium* Hooker and Arnold. It is named to honor Helen Sharsmith whose major contribution to the knowledge of *Hesperolinon* morphology and ecology has not been equaled.

DISCUSSION

Hesperolinon sharsmithiae superficially resembles three other *Hesperolinon* species: *Hesperolinon clevelandii* (Greene) Small, *H. tehamense* H. Sharsmith, and *H. bicarpellatum* H. Sharsmith. All have yellow flowers, linear, non-clasping cauline leaves, and a diffuse inflorescence. Table 1 compares the morphology of *H. sharsmithiae*, *H. clevelandii*, *H. bicarpellatum*, and *H. tehamense*. In addition to the traditional morphological features, the comparison includes the description of a floral structure that surrounds the base of the ovary that is called the "cup", illustrated in Fig. 2. (In Linaceae, the staminal filaments are basally fused to form a cup that surrounds the base of the ovary.) The five petals of *Hesperolinon* species attach at the rim of the cup, alternating with the filaments, but unlike the filaments, they are attached very lightly and are easily detached. The rim of the cup is lobed between the alternating filament/petal attachments. The comparison also includes the base of the petals and the petal base appendages. For example, the petal appendages in *H. clevelandii* are either poorly developed or absent, while they are well developed in *H. sharsmithiae* and *H. bicarpellatum*.

TABLE 1. MORPHOLOGICAL COMPARISON OF FOUR *HESPEROLINON* SPECIES. Data from Sharsmith (1961) and Personal Observation.

	H. sharsmithiae	*H. clevelandii*	*H. bicarpellatum*	*H. tehamense*
Height of Plant (cm)	5–50 cm	5–15 (–30) cm	10–30 (–70) cm	20–35 cm
Habit	Erect, widely spreading, diffuse	Erect, widely spreading, diffuse	Erect, widely spreading, diffuse	Erect, widely spreading
Stem	Dichotomous from middle, pubescent above nodes	Branched from middle, pubescent above nodes	Dichotomous from middle, pubescent above nodes	Primary branches alternate, secondary dichotomous, often pubescent
Inflorescence	Dichasial cyme	Monochasial cyme	Dichasial cyme	Usually monochasial
Inflorescence bracts	Opposite	Alternate	Opposite	Opposite to alternate
Leaves	Alternate, linear, glabrous, 15–20 mm long, 1–1.5 mm wide	Lower tomentose;10–15 mm long, 2–2.5 mm wide	Alternate, linear, glabrous, 15–20 mm long, 1–1.5 mm wide	Cauline alternate and linear, 10–20 mm long, 1–2 mm wide
Stipular glands	Conspicuously present	Inconspicuous	Present, lower nodes only	Present, inconspicuous, or absent
Pedicels	Less than or equal to 5 mm.	(2) 5–25 mm	5–7 mm (–20)	0.5–2 mm in flower, longer in fruit
Sepals	Five, equal, oblanceolate, sparsely glandular on margins; 3 mm	Oblanceolate, unequal, inner 1.5–2.5 mm, outer 2.5–3 mm, erect or reflexed at tip	Five, equal, lanceolate, sparsely glandular on margins; 1.5–2 mm	2–3 mm long, lanceolate, usually spreading at tips, sometimes puberulent
Petals	3–4.5 mm long; 2–2.5 mm wide; yellow, sometimes red streaked at midvein; oblanceolate to obovate nearly oval, always erose, spreading at anthesis	1.5–2.5 mm; yellow, red streaked at midvein; oblanceolate, slightly expanded at anthesis	2.5–4 mm long; yellow, red streaked; oblanceolate to obovate nearly oval, spreading at anthesis	4–5 mm long, 3–4 mm wide, obovate, often notched at apex, usually widely spreading, bright yellow tinted orange or red
Petal Appendages	Claw with appendages, well developed, sometimes hispidulous	Claw with appendages poorly developed	Claw with appendages well developed; hispidulous	Claw with appendages well developed, the horizontal crest and ligule often hairy
Petal cup	Yellow, 10-lobed	Yellow, glabrous, 5-lobed	Yellow, 10-lobed	Yellow, rim often hairy,10-lobed
Filaments	Five, yellow, 1.5–2.5 mm. exserted, spreading at anthesis	Five, yellow, 1–2 mm, included	Five, yellow, 2.5 mm, exserted	Five, 3–4 mm long, yellow, spreading, exserted, usually very hairy at base
Styles	Three, 2–3.5 mm., exserted	Three (seldom two), 0.5–1 mm; included	Two (sometimes three); 3 mm, exserted	Three, 3.5–4.5 mm long, spreading, exserted
Fruit	Globose-ovoid capsule, about 2 mm high and 2 mm wide	Globose-ovoid capsule 2–3 mm long, 2–2.25 mm wide	Globose-ovoid capsule 2–3 mm long, 2–2.25 mm wide	Globose-ovoid capsule 2–3 mm long, 2–2.25 mm wide

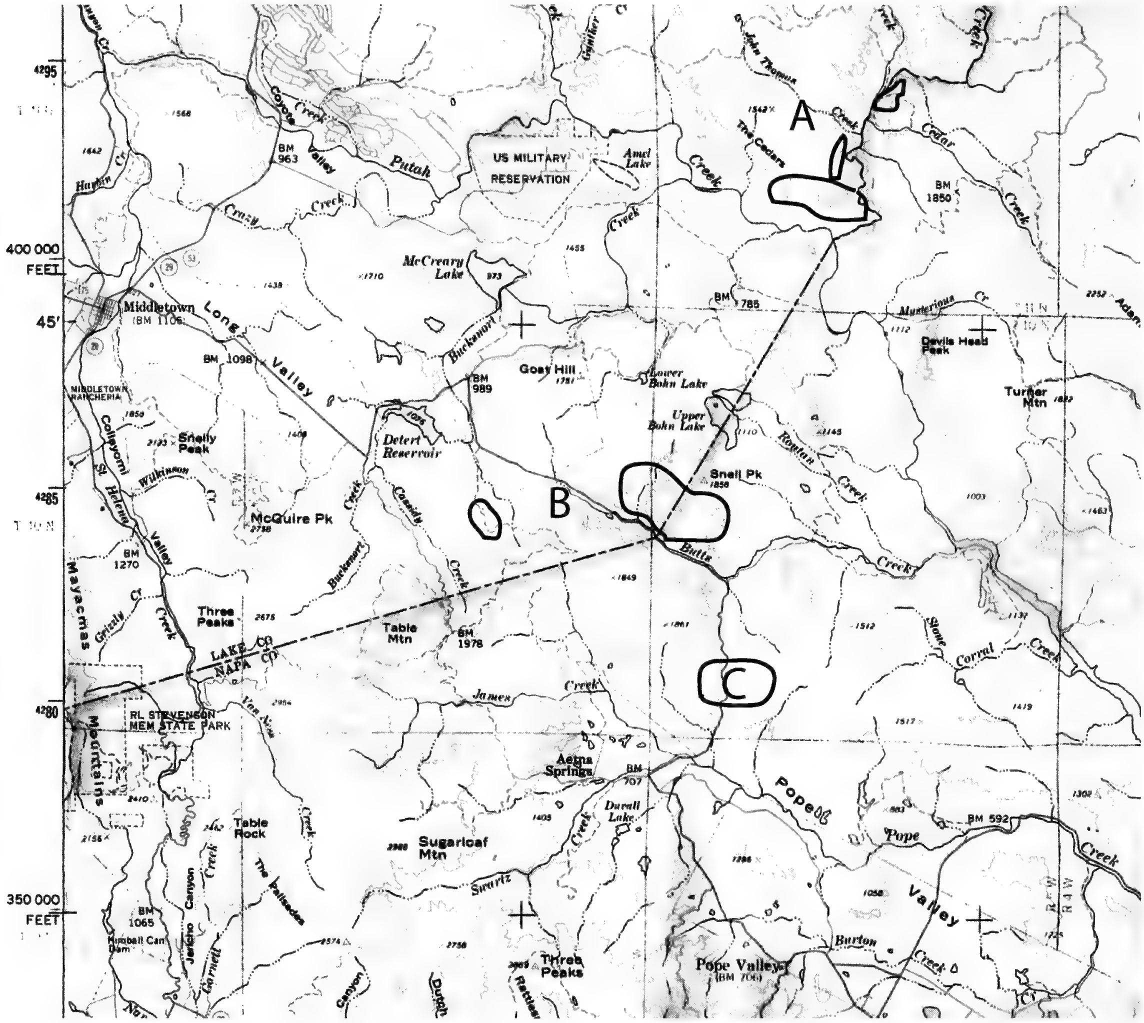

FIG. 1. Populations of *Hesperolinon sharsmithiae*, *H. bicarpellatum*, and Intermediates known to the author. Legend: *H. sharsmithiae*: A, *H. bicarpellatum*: B, and Intermediates: C.

Comparative Morphology

No genetic analyses of the *Hesperolinon* species have been published. Notwithstanding the lack of this valuable data, comparative morphology is sufficient to establish the distinctiveness of *H. sharsmithiae*. Table 1 compares the morphology of *H. sharsmithiae* with the morphology of the three similar yellow-flowered *Hesperolinon* species that grow in the vicinity.

I have omitted from the comparison *H. serpentinum* McCarten, a taxon that was first referred to in the Jepson Manual (Hickman 1993), because it was not accompanied by a formal description and a type specimen was not designated for it, and thus the name is effectively illegitimate. However, I examined specimens at the Jepson Herbarium that are labeled *Hesperolinon serpentinum* and found similarities between those specimens and *H. sharsmithiae*.

The Jepson Herbarium houses five specimens labeled *Hesperolinon serpentinum*. Two of the specimens (Taylor 14933, 14952) are from Stanislaus County and generally resemble *H. sharsmithiae*, except that the inflorescence bracts of the former are single and very narrow, while those of the latter are opposite and wider. Other specimens (Taylor 16669 – multiple plants) were collected near Butts Canyon in Lake County. They appear to be *H. bicarpellatum* displaying the intermediate tricarpellate character discussed above. The characters of the remaining specimen, collected by Jepson and later labeled *Hesperolinon serpentinum*, are too indistinct to determine the species. Jepson collected it at a place called "La Brusca" on Howell Mountain in Napa County. The soil at La Brusca is volcanic; *H.*

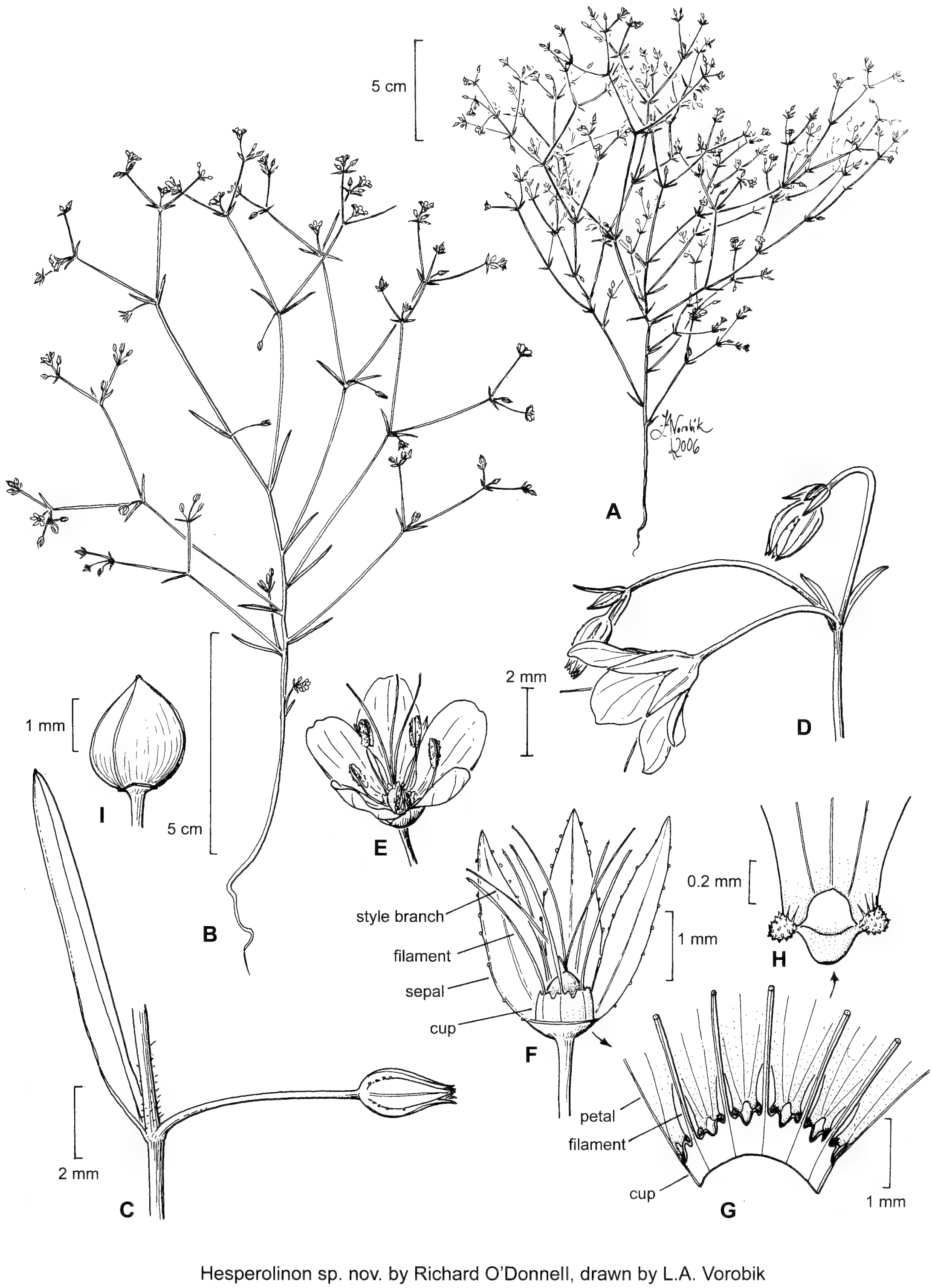

FIG. 2. *Hesperolinon sharsmithiae*. A. Typical habit, fairly dense, diffuse inflorescence. B. Habit simplified to more clearly depict the strictly dichotomous branching. C. Cauline puberulence confined as usual to the internodes above the leaf axils. D. Buds and partly open flower. E. Open flower with three exserted styles. F. Cross section of calyx illustrating placement of cup. Note sparse glandulosity on sepal margins. G. Cup with filaments and petals attached. H. Petal base. I. Fruit.

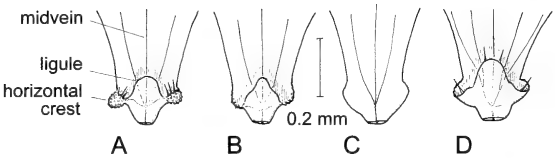

FIG. 3. Petal bases: A. *Hesperolinon sharsmithiae*, B. *H. bicarpellatum*, C. *H. clevelandii*, D. *H. tehamense*. The illustration of *H. sharsmithiae* and *bicarpellatum* are from fresh specimens. The lateral appendages of *H. sharsmithiae* and *H. bicarpellatum* are frequently more alike than depicted. *H. clevelandii* and *tehamense* are based on illustrations in Sharsmith.

serpentinum is reported only from serpentine soils while *H. clevelandii* is found on both serpentine and volcanic soils. Thus, this specimen is more likely to be *H. clevelandii* than *H. sharsmithiae*. *Hesperolinon sharsmithiae* and the invalid "serpentinum" may be the same entity but the material housed at the Jepson Herbarium does not provide material support for that position. The California Academy of Sciences herbarium has no specimens that are labeled *H. serpentinum*.

I also examined specimens of *H. tehamense* at the California Academy of Sciences herbarium and at the Jepson Herbarium. This species is narrowly distributed in Tehama and Glenn Counties. Its floral parts are generally larger than those of *H. sharsmithiae* and it is frequently pubescent throughout — a light vestiture that gives it a hoary appearance — which *H. sharsmithiae* lacks; *H. sharsmithiae* is glabrous, except at the nodes. In addition, the cup and petal appendages of *H. sharsmithiae* differ from those of *H. tehamense* as shown in Fig. 1.

The descriptions of the three species compared to *H. sharsmithiae* in Table 1 are abbreviated versions of Sharsmith's very detailed descriptions (Sharsmith 1961). They do not always agree with the details in the descriptions in The Jepson Manual (Hickman 1993) or Munz and Keck (1959, 1968) but the differences are not material.

Relationship to *Hesperolinon Bicarpellatum*

Hesperolinon sharsmithiae may be closely related to *H. bicarpellatum*, with which it shares diagnostic characters as shown in Table 1.

Their known ranges overlap northeast of Middletown but otherwise differ (Fig. 1). *Hesperolinon bicarpellatum* flourishes in and around Butts Canyon, southeast of Middletown. *Hesperolinon sharsmithiae* is abundant on both sides of Hunting Creek south of Paradise Valley, particularly in an area called The Cedars, northeast of Middletown. Butts Canyon and the Cedars are separated by the largely volcanic blue oak savannah of Guenoc.

The number of styles is the primary distinguishing field character: the former has three styles and the latter two. However, some individuals and populations of *H. bicarpellatum* just southeast of Butts Canyon display a partial tricarpellary condition.

The extensive populations of *H. bicarpellatum* in Butts Canyon (Fig. 1) are uniformly bicarpellate. Plants bearing both bicarpellate and tricarpellate flowers begin to occur on the ridge between Butts Canyon and Pope Valley (pers. obs.) and continue to occur to the southern end of its known distribution in Steele Canyon. Sharsmith (1961) observed this phenomenon and described the tricarpellary condition as "intermediate" and "…never completely 3-carpellary". Specifically, she reports a maximum of 50% tricarpellary flowers on individuals of *H. bicarpellatum*.

I sampled individual plants from four populations on the ridge between Butts Canyon and Pope Valley (Fig. 1), in the vicinity of a site that I had sampled in previous years and found to be intermediates. I examined 14 plants, dissected all of the open flowers, nearly open buds, and very young buds of each plant and found that 330 buds out of 339 buds examined—over 97%—were tricarpellate. This is a much higher proportion of tricarpellate flowers than Sharsmith observed. Although I did not observe other intermediate characters in these populations, additional studies of the populations in this area and annual monitoring may reveal other intermediate characters and help to clarify the relationship of these intermediate populations to populations of *Hesperolinon sharsmithiae* and *H. bicarpellatum*. I have found no bicarpellary flowers among the extensive Hunting Creek populations of *H. sharsmithiae*.

Conclusion

Hesperolinon sharsmithiae is a new species that differs from *H. bicarpellatum* in style number, number of carpels and ovules, and petal size; it differs from *H. tehamense* in petal size, vestiture, length of pedicel; it differs from *H. clevelandii* in the development of petal appendages, petal size, and edaphic preference. It most closely resembles and may be related to *H. bicarpellatum*.

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NOTEWORTHY COLLECTIONSS

ARIZONA

PORTERELLA CARNOSULA (Hook. & Arn.) Torr. (CAMPANULACEAE).—Coconino Co., AZ, Fort Valley, just SW of the lower flanks of the San Francisco Peaks, Coconino National Forest. Plants dominating several small swales, growing in wet soil from desiccated ephemeral pools. UTM zone 12, 432968 E, 3902771 N, ca. 2225 m, with *Geum triflorum*, *Poa pratensis*, *Ranunculus cardiophyllus* var. *cardiophyllus*, *Plagiobothrys scouleri* var. *hispidulus*, *Limosella acaulis*, *Eleocharis ovata*, *Myosurus apetalus* var. *montanus*. 22 June 2005, *K. Christie 788* (ASC).

Previous knowledge: AZ, UT, CA, NV, OR, ID, WY.

Significance: First collection in AZ since 1927.

CRYPTANTHA MINIMA Rydb. (BORAGINACEAE).—Coconino Co., AZ, Babbitt Ranches, ca. 4.5 km W of Double Top, private land. Plants growing on a flat, open slope in fine-textured clay-based soil. UTM zone 12, 408389 E, 3941541 N, ca. 1875 m, with *Pinus edulis*, *Juniperus monosperma*, *Gutierrezia sarothrae*, *Bouteloua gracilis*. 10 June 2005, *K. Christie 641* (ASC).

Previous knowledge: TX, OK, NM, CO, KA, NE, SD, WY, MT, mostly on the plains east of the continental divide.

Significance: First record for AZ; range extension of ca. 500 km W and SW respectively, from central NM and southwest CO populations.

SUCKLEYA SUCKLEYANA (Torr.) Rydb. (CHENOPODIACEAE).—Coconino Co., AZ, Red Lake, ca. 3.5 km W of Cedar Mountain, private land. Plants growing in disturbed, wet soil/mud at the edge of a lake. UTM zone 12, 394613 E, 3915285 N, ca. 1975 m, with *Rumex salicifolius*, *Gnaphalium exilifolium*, *Limosella acaulis*, *Coreopsis tinctoria*, *Elatine brachysperma*, *Eleocharis palustris*. 16 September 2005, *K. Christie 1193* (ASC).

Previous knowledge: TX, OK, NM, CO, KA, NE, ND, WY, MT.

Significance: First record for AZ; range extension of ca. 300 km W from Catron Co., NM.

PANICUM MOHAVENSE J. Reeder (POACEAE).—Coconino Co., AZ, Babbitt Ranches, Rabbit Canyon, private land. Plants growing in small pockets of soil on a limestone bench. UTM zone 12, 427392 E, 3939582 N, ca. 1975 m, with *Pinus edulis*, *Juniperus monosperma*, *Gutierrezia sarothrae*, *Bouteloua gracilis*. 3 October 2005, *K. Christie 1300* (ASC).

Previous knowledge: Mohave Co., AZ; and seen in 1998 in Socorro Co., NM.

Significance: New locality for a critically imperiled (G1) species; first record for Coconino Co.; range extension of ca. 250 km E from Mohave Co., AZ.

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CALIFORNIA

BITUMINARIA BITUMINOSA (L.) Stirton (FABACEAE).—Los Angeles County, cismontane foothills of the San Gabriel Mountains: *Wesley O. Griesel s.n.* RSA, 11 April 1961, Millard Canyon, ca. 2000 ft. elev.; *Wesley O. Griesel 620* RSA, 28 May 1962, same location; *Philip A. Munz 24319* RSA, 29 May 1962, same location; *R.F. Thorne 41500* RSA 18 Mar 1971, Cobal Canyon, 3 miles N of Claremont, ca. 1650 ft. elev.; *S. Hobbs 1* (RSA, UCR), 22 Apr 1999, Clamshell Truck Trail above Monrovia, barely invading into chaparral, proliferating in disturbed soil on roadsides. *V. Soza et al. 1308* (RSA) 28 Jun 2001, Forest Service Road 2N66, between Fern Canyon and Pine Canyon (ca. 2600 ft. elev., T2N, R12W S 29, north of Altadena). *V. Soza & LeRoy Gross 1140* (RSA) 18 Apr 2001, Santa Anita 1999 fire area, between Little Santa Anita and Santa Anita Canyons, north side of Santa Anita Canyon Road along edges of minor canyon bottom ca. 1300 ft. elev. *Scott D. White 9827* (RSA) 14 Oct 2003, "Auburn" debris basin at northern terminus of Auburn Ave., sterile seedling shrub, solitary in sand of debris basin floor (the single plant collected as the voucher; De Vries and Warniment also saw *B. bituminosa* there in 2005 but did not collect it). *Scott D. White 9831* (RSA, UCR, duplicates to be distributed), 14 Oct 2003, "Carter" debris basin at the northern terminus of Baldwin Ave, about 10 shrubs in a cluster, growing in upland well above the debris basin margin, at edge of adjacent coastal sage scrub, many seedlings and a few mature shrubs also on the basin floor. *Scott D. White 9839* (RSA, duplicates to be distributed), 22 Oct 2003, "Sierra Madre" debris basin at the northern terminus of Sumac St., a few plants on sandy slope above the ephemeral stream channel, just upstream from the debris basin; well past flowering and only calyces of earlier flowers present. *P. De Vries & A. Warniment s.n.* (RSA, not yet accessioned), 24 Mar 2005, "Lannan" debris basin just west of Santa Anita Canyon Road in Sierra Madre, growing on uplands in two patches totaling about one-quarter acre, surrounded by chaparral and coastal sage scrub, with little evidence of soil disturbance. *Lee Jones s.n.* (UCR) 14 May 2005, above Stone House Road and Kaia Lane in Sierra Madre (near "Lannan" debris basin, above), disturbed soil at edge of trail. *A. Warniment s.n.* (RSA, not yet accessioned), 15 July 2006, Monrovia Canyon Park, along trail between Nature Center and waterfall, about 100 yards from Nature Center at first switchback, several plants in drainage below culvert, between chaparral and oak woodland.

Los Angeles County, San Raphael Hills (eastern end of the Verdugo Mountains, between Glendale and Pasadena): *David Bramlet 3526* (RSA), 1 Oct 2003, "Chamberlin" Debris Basin, about 1.5 km WNW of the Rose Bowl, about 1200 ft. elev.; ca. 5 plants.

Previous knowledge. Treated as *Psoralea bituminosa* L. in Munz 1968 (*Supplement to A California Flora*, UC Press Berkeley) and 1974 (*Flora of Southern California*, UC Press, Berkeley). Native to southern Europe, Spain east to Turkey and Crimea (T.G. Tutin et al. 1968, *Flora Europea* vol. 2, Cambridge Univ. Pr., London) and the Canary Islands (J. Izquierdo et al. 2001, Lista de especies silvestres de Canarias, *La Laguna* 100–140). Wesley O. Griesel collected the first known North American specimens at Millard Canyon in 1961. Philip

A. Munz visited the site with him in 1962 and distributed specimens to several major North American herbaria (P. Munz 1963 *Aliso* 5:354). Munz (1968 *op. cit.*, 1974 *op. cit.*) reported it "possibly established after being tested as a fire-resistant plant by Forest [Service] personnel" at Millard Canyon in the San Gabriel Mountains and at Pleasanton in Alameda County. Excluded from The Jepson Manual (Hickman, 1993, UC Press, Berkeley) as "apparently not naturalized." Excluded by Isely [1998: Native and Naturalized Leguminosae (Fabaceae) of the United States, Monte L. Bean Museum, BYU, Provo, UT] as "sporadically cultivated, waif, or possibly established in disturbed areas." Mentioned by J. W. Grimes in his *Pediomelum* treatment (Hickman 1993, p. 640) as possibly naturalized in the San Bernardino Mountains. We have found no specimens or other written reports from the San Bernardino Mountains, but habitat there is much like the San Gabriels and *B. bituminosa* certainly could occur there. Its flowers and foliage are attractive during spring. It may be tempting for use in drought-tolerant landscaping, though it dies back in summer. It is grown agriculturally for forage and other purposes at many locations worldwide and as an ornamental in England (mentioned on a personal web site by Jonathan Garret, 31 Mar 2004). The USDA Natural Resource Conservation Service includes it in a list of noxious and invasive species (http://plants.usda.gov/java/introduced?) but it is not listed as a noxious weed by the California Department of Food and Agriculture (http://www.cdfa.ca.gov/phpps/ipc/weedinfo/winfo_list-synonyms.htm).

Significance. Bituminaria bituminosa has become established at several sites in the cismontane San Gabriel Mountains and at least one site in the San Raphael Hills. Several collections cited here were made during field surveys of flood control debris basins, but they do not imply that *B. bituminosa* occurs primarily in these basins. It was generally in open areas disturbed by debris basin maintenance or seasonal flows along ephemeral channels. The label on Griesel's original specimen noted that it was growing with *Spartium junceum*, an alien species characteristically invasive along washes and roadsides. *Bituminaria bituminosa* probably occurs in sandy washes, roadsides, and upland shrublands throughout the foothills above Altadena, Sierra Madre, Arcadia, and Monrovia. If Millard Canyon was the only anthropogenic introduction above Altadena, then *B. bituminosa* has dispersed eastward at least 15 km and crossed several watershed boundaries between Altadena and Monrovia. It also may have dispersed a few km south to the San Raphael Hills via open space around Devil's Gate Reservoir and the Arroyo Seco flood control channel. Dispersal to this site also would have required upslope movement across some residential areas. The Cobal Canyon site is about 25 km east of the other locations, suggesting that undocumented *B. bituminosa* occurrences may be found in the intervening foothills or that a second anthropogenic introduction was made, possibly in the San Dimas Experimental Forest a few km north.

Based on its Mediterranean origin, its dispersal patterns to date, and its regular occurrence in soils disturbed by natural hydrology or mechanical equipment, *Bituminaria bituminosa* seems capable of spreading throughout the mountains and foothills in cismontane southern California and northern Baja California, especially if it is ever used for landscaping in the foothill communities.

We thank Dieter Wilken for reviewing an earlier draft of this note.

—Scott D. White, Scott White Biological Consulting, 201 N. First Ave., No. 102, Upland CA 91786 and Andrea Edwards, Bonterra Consulting, 3452 E. Foothill Blvd., Suite 420, Pasadena, CA 91107.

MADROÑO, Vol. 53, No. 4, p. 411, 2006

REVIEW

Living with the changing California coast. Edited by Gary Griggs, Kiki Patsch, and Lauret Savoy. 2005. University of California Press, Berkeley, CA. 540 pp. Hard cover $60.00, ISBN 978-0-520-24445-0; Paperback $24.95, ISBN 978-0-520-24447-4.

Living with the Changing California Coast, is a revised version of the book by the same title that originally was published in 1985. This version has been revised substantially and updated to include the latest data on human activity along the coast, as well as the latest theories on climate change and its influence on rising sea levels and shoreline processes. It contains 279 black and white photographs and 81 maps. Text material contributed by the editors is enhanced by an additional 15 contributors.

The first eight chapters of this volume deal with geologic evolution of the coastline, climate and weather, shoreline processes, and the implications of coastal hazards on land ownership. Chapter 3 is all about climate and weather. It is written in a manner that is fully understandable to non-meteorologists. The authors describe the types and sources of the storms that bring precipitation to California. Recent storm events are explained. El Niño is fully explained. A series of simple graphics helps to explain seasonal changes in the weather, tides, and the history of changing sea level. Chapter 4 describes shoreline processes such as erosion, the work of currents and waves, as well as the sources and losses of sand. Chapter 7 is about what humans have done to combat the forces of nature and the extent to which their attempts have been effective.

The remainder of the book is divided into twelve chapters that discuss the California coastline region by region from north to south. For example, Chapter 9 covers the region from the Oregon border to Shelter Cove and Chapter 20 covers from Dana Point to the international border. Each of these regional chapters is further divided into descriptions of subregions and detailed maps, and include summaries of the characteristics, threats, and public policies relevant to each specific region. For example, if you were considering owning property on the coast near Pismo Beach you could refer to the specific map of the region in Chapter 16. You would be informed that the Shell Beach area has many homes on a narrow marine terrace that require protection by seawalls, bulkheads, rip rap, etc. and that seacliff retreat averages four to eight inches per year.

Essentially, this is a geology book. Botanists, however, do live near the coast and many of them are homeowners that are influenced by coastal processes. In fact, demographic data have told us that a full 80 percent of California residents live within an hour's drive of the coast, and the authors in their discussion of global warming point out that 60 percent of the world's population lives within 35 mi of a coastline and that 100 million people live within three vertical feet of sea level. Coastal plants are influenced by climate, weather, soil, and coastal processes. Do you want to know why the coastal dunes (and by extension their endemic plants) are located where they are? It's in this book. Whether you are a botanist or not, if you are interested in coastal natural history and the implications of living near the coast, you should own this book. Periodic online sales advertised by University of California Press offer this book at substantial discounts in hard cover or paperback.

—ALLAN A. SCHOENHERR. Professor of Ecology, Emeritus, Fullerton College, 321 E. Chapman Avenue, Fullerton, CA 92832. Email: Aschoenherr@fullcoll.edu

MADROÑO, Vol. 53, No. 4, p. 412, 2006

PRESIDENT'S REPORT FOR VOLUME 53

As I take over the presidency from the able hands of Mike Vasey, I am pleased to report that the California Botanical Society continues in good health.

I would like to thank the officers and council members for their continued efforts to keep the Society vibrant and relevant. Every year we all seem to get a little bit busier. So, the commitment of people who find time in their overbooked schedules to build and sustain the Society is all the more laudable.

A primary reason for the continued success of the Society is the quality of our quarterly publication, Madroño. John Hunter, the editor of Madroño, deserves our kudos for the quality of the journal, as do the contributing editors, authors, and reviewers whose concrete efforts embody our mission of advancing Western American botany. This year, a special issue of Madroño appeared with a flora of the liverworts and hornworts of California. This is a companion volume to the two issues on the moss flora published in 2004. This set comprises a complete bryoflora of the state and will be an important reference for decades to come. John Hunter's term as editor extends through 2007, but we are looking for a new editor in order to effect a seamless transition. If you are interested in making a truly lasting contribution to our field, or if you know of an excellent candidate, please contact John Hunter or me regarding the future editorship.

The most significant project of the past year has been preparing for online publication of the journal. Corresponding Secretary Sue Bainbridge, along with Bruce Baldwin and Jim Shevock, spent many hours researching possible approaches and finally recommended that the Society partner with BioOne to make Madroño articles available through an online service. This exciting development, one that we have anticipated for some time, should take place by the publication of the first issue of Madroño next year. Web access to articles will increase the visibility and impact of articles published in Madroño and will increase the frequency of their citation as well. This, in turn, is certain to increase the number of articles submitted for publication, a move that will help maintain the high quality of the journal. Finally, online access will increase the ability of those botanists who work at facilities without extensive libraries to have immediate access to articles. This important transition will have somewhat unpredictable effects on the long-term finances of the Society. Although online publication will result in new revenue streams for the Society, many botanical societies have seen a decrease in institutional memberships after going online. This fact, combined with ever-increasing publication costs, will create a challenge to keep membership and subscription affordable. Increasing our endowment is one way that we can continue to provide our members with low cost access to benefits. If you can afford it, please consider giving to the endowment fund while renewing. A contribution to the future of botany is a lasting and worthwhile investment.

Another way to help the Society is by encouraging your colleagues to become members. There is no time like the present to do your part. Incidentally, if you haven't renewed your membership yet, please take the time to do so right now. Timely renewals avoid confusion, added costs, and wear-and-tear on our volunteers.

I encourage everyone to attend the Society's biennial graduate student meeting and annual banquet at the California Polytechnic University in San Luis Obispo on Saturday February 17, 2007. San Luis Obispo is a charming town and an excellent venue for a meeting. Second Vice-President Matt Ritter will be coordinating this event. At the graduate student meeting, held during the day, students from different institutions will be presenting their research proposals, research-in-progress, or completed research in botany in a standard scientific-meeting format. These meetings are always interesting and provide an excellent opportunity to see the future direction of botanical research. In the evening, at the annual banquet, we will have the great pleasure of hearing Constance Millar, Research Paleoecologist for the USDA Forest Service, speaking on the history of climate change in California. In this period of justified alarm, we will find some comfort in taking a longer view of these issues.

The mission of the Society reaches beyond the political boundaries of California to all of Western America. The Annetta Carter fund was established to provide seed money for plant research in Baja California, Mexico. In 2006, Peter Garcia used funds from the Annetta Carter Fund to make important collections of plant specimens in Baja California. These specimens will contribute to the ongoing Flora of Baja California Project at the San Diego Natural History Museum. If you wish to contribute to the Fund, you can give a line item contribution via the membership form. Another way in which the Society furthers its mission is by occasionally sponsoring important symposia at professional meetings. In June 2006, we sponsored "Ecological Restoration in a Changing World: Case Studies from California", a symposium at the National Society for Conservation Biology meeting in San Jose. Council member Jeff Corbin and then-President Mike Vasey performed all the heavy lifting in arranging this symposium. Look for articles arising from this meeting in future issues of Madroño.

First Vice-President Stephania Mambelli continues to do a great job of assembling a first-rate roster of speakers for our monthly meetings in Berkeley. This year's speakers have included Todd Keeler-Wolf (CDFG), Mark Brunell (U Pacific), Debra Ayres (UC Davis), Radika Bhaskar (Stanford), and Jarmila Pittermann (UC Berkeley). Refreshments are being offered before and after the meetings to facilitate socializing and discussion. Attendance has been high so far. So, if you are not too far away from Berkeley, please come to a meeting or two. I am sure you will enjoy it. Another enjoyable occasion was the annual banquet in February, 2006 in Claremont, California. I would like to thank Second Vice-President Travis Columbus, of the Rancho Santa Ana Botanic Garden, for planning this delightful event. It was enjoyed by all who attended; the banquet speaker, Jon Keeley, talked about his research on fire ecology, a central ecological phenomenon in California.

I also thank Recording Secretary Staci Markos, student representative Vicente Garcia and ex-president Bruce Baldwin for their dedicated commitment and contributions to furthering the goals of the Society, and to all of our members for your continuing support. I wish you all a great year in 2007, as well as a wonderful botanical field season.

DEAN G. KELCH
December, 2006

MADROÑO, Vol. 53, No. 4, p. 413, 2006

EDITOR'S REPORT FOR VOLUME 53

I am pleased to report that during 2006 the number of manuscripts submitted to *Madroño* was comparable to previous years, and that the California Botanical Society has published another volume of *Madroño* reporting research on the flora and vegetation of western North America.

During the last twelve months, 42 manuscripts were submitted. Of these manuscripts, 4 were rejected, 8 had major revisions requested, 22 were accepted with minor revisions, and 8 manuscripts are still in review. Of those accepted with minor revisions, 15 were published in this volume. The interval from submission to publication has been approximately one year long. During 2006, 3 book reviews and 10 noteworthy collections (revising the geographic range of 27 species) also were submitted, and 9 of these have already been published.

Volume 53 reports the research of 78 different authors. Two of these authors, William T. Doyle and Raymond E. Stotler, produced an annotated species catalog with keys for the liverworts and hornworts of California. This catalog was published as Issue 2 of this volume.

Authors were aided by numerous reviewers (including Ken Kellman, Jim Shevock, Wilf Schofield, and David Wagner who reviewed all of Issue 2), an editorial board, Jon Keeley (Book Review Editor), Dieter Wilken (Noteworthy Collections Editor), Margariet Wetherwax (Noteworthy Collections Editor), Steve Timbrook (Compiler for Annual Index), Annielaurie Seifert and her colleagues at Allen Press, and the Executive Council of the California Botanical Society. All of these individuals deserve to be recognized and thanked for their contributions to *Madroño*.

John C. Hunter
September 21, 2006

Madroño, Vol. 53, No. 4, p. 414, 2006

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Classified entries: major subjects, key words, and results; botanical names (new names are in **boldface**); geographical areas; reviews, commentaries. Incidental references to taxa (including most lists and tables) are not indexed separately. Species appearing in Noteworthy Collections are indexed under name, family, and state or country. Authors and titles are listed alphabetically by author in the Table of Contents to the volume.

MADROÑO, Vol. 53, No. 4, p. 417, 2006

DEDICATION

Daniel H. Norris

This volume of *Madroño* is dedicated to Daniel H. Norris. Dan obtained his PhD in 1964 from the University of Tennessee from bryologist Jack Sharp. His first teaching assignment upon graduation was at Catonsville Community College (Baltimore area). Dan first arrived in California in 1967 as Assistant Professor at Humboldt State University. Over the next 24 years, he taught various plant morphology, taxonomy, and bryology courses until his official retirement in 1991. While at Humboldt State, he guided and directed over a dozen graduate students, many obtaining masters' degrees specializing in bryology. Several of his students are now university professors themselves.

Dan's passion for fieldwork is boundless. Over his career, he has made more than 109,000(!) bryophyte collections, not just from California, Intermountain West, Alaska and British Columbia, but from the Caribbean (Dominican Republic, Puerto Rico), Mexico, South America (Argentina, Ecuador), Middle East (Iran), Scandinavia, tropical Africa (Equatorial Guinea), Malesia (Papua New Guinea), Pacific Islands (Moorea, Tahiti, Fiji, New Caledonia), Australia and New Zealand. Duplicates of his collections reside in all of the major bryophyte herbaria.

Upon his retirement, Dan had many options to continue his bryological research at Oregon State University, University of Washington, or the University of Helsinki but he eventually decided to transfer his bryophyte collection to the herbarium of the University of California, Berkeley, where he became a research associate in 1993. It was during this tenure where Dan began to teach Jepson Herbarium workshops for bryophytes and the genus *Carex*. He also conducted bryophyte identification workshops primarily designed for Forest Service botanists who desired to add these gametophyte dominant plants to agency conservation and biodiversity programs. A new cadre of bryological amateurs blossomed during these efforts that created a renaissance for California bryology. In short order, new bryophyte distribution records across the state were being documented by these field-oriented botanists along with the discovery of species new to science.

Throughout his career, Dan has published numerous papers adding to the overall understanding and knowledge of bryophyte distribution patterns based on his extensive field work and collecting activities. The ongoing series of bryophyte floristic treatments for the Huon Peninsula, Papua New Guinea written in collaboration with Dr. Timo Koponen, University of Helsinki is an extremely significant work for all bryologists with interest in Melasian and Southeast Asian mosses. One of Dan's greatest experiences occurred in 1990 when he was presented an honorary PhD by the President of Finland on the occasion of the 350th anniversary celebration of the University of Helsinki.

Although Dan's bryophyte collecting expeditions spanned most continents, it is his love for the California Floristic Province where he has spent the majority of his career to document its bryoflora (see Madroño **51**: 1–131; 133–269). Dan has been involved in the naming of over 40 bryophytes as new to science including the moss genera *Bryolawtonia*, *Orthothuidium*, *Stoneobryum* and *Unclejackia*. Species named in his honor include a Mexican legume, 16 bryophytes, and the moss genus *Bryonorrisia*.

Photo by Staci Markos, courtesy of the Jepson Herbarium, June 2003.

Those who meet Dan for the first time quickly experience his unique brand of humor and soon realize that he is an exceptional scientist who will share his passion for bryophytes with anyone showing an interest. It is with great pleasure that Volume 53 of Madroño is dedicated to Dan Norris for his lifetime achievements and professional dedication to these remarkable gametophyte dominant plants.

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PATTERNS OF POSTFIRE REGENERATION IN A SOUTHERN CALIFORNIA MIXED CHAPARRAL COMMUNITY

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ABSTRACT

Effects of prefire stand age, fire intensity, and hillslope position on postfire vegetation recovery during the first two postfire seasons were studied in two contrasting stands of mixed chaparral at San Diego State University's Sky Oaks Field Station (San Diego County, CA). One stand was approximately 60-years old and the other 12-years old when both burned in the July 2003 Coyote Fire. The two stands showed contrasting patterns of postfire community composition among different plant groups based on their modes of postfire regeneration. Fire intensity was significantly higher in the older stand. Increased fire intensity was positively correlated with establishment of seedlings of *Ceanothus greggii* var. *perplexans* (an obligate seeder), and negatively correlated with seedling abundance of *Adenostoma fasciculatum* (a facultative seeder). Hillslope position was also important in determining patterns of abundance, suggesting that soil erosion and deposition following fire may have a significant effect on postfire community recovery on these steep sites. Alternatively, prefire differences in the chaparral community that were correlated with hillslope position may account for these differences. The postfire herbaceous community in the first year was dominated by *Phacelia brachyloba*, a fire annual. Contrary to expectations, this species was found in greater abundance in the old stand than in the young. Fire annuals were largely absent from the community in the second year, and were replaced in abundance by a variety of opportunistic native and exotic annuals.

Key Words: *Adenostoma fasciculatum*, chaparral, *Ceanothus greggii*, Coyote Fire, facultative seeder, fire, fire annual, obligate seeder, Sky Oaks Field Station, San Diego County.

Chaparral, an evergreen, sclerophyllous shrubland that dominates in Mediterranean-type climate areas of California, is found in the inland foothills of San Diego County, primarily on steep slopes between 150 and 1400 m elevation. Wildfires are a common feature of the chaparral environment, and the community as a whole is resilient to wildfire (Horton and Kraebel 1955; Hanes 1971; Keeley 1991; Conard and Weise 1998). Chaparral fires are usually stand-replacing crown fires. Vegetation recovery occurs through postfire resprouting from belowground vegetative parts (e.g., root crowns or basal burls; Zedler 1981; Zammit and Zedler 1992) and/or through seedling establishment from soil-stored seeds (Keeley 1986, 2000). Under most burning regimes, community structure is altered only briefly following a burn, and species composition does not change significantly from one fire cycle to the next (Keeley 1991).

Investigating variation in plant groups based on regenerative and/or growth form attributes can provide a link between vegetation responses to disturbance and the effects of these changes on overall community properties and function (Kleyer 1999; Lavorel et al. 1999; McIntyre et al. 1999; Pausas 1999; Guo 2001; Lloret and Vilá 2003; Rusch et al. 2003). California chaparral species show a continuum of postfire regeneration modes from those that regenerate only by resprouting (obligate resprouters) to those that regenerate only from seeds (obligate seeders; Keeley and Zedler 1978; Lavorel et al. 1999; Pausas 1999). Some species are able to both resprout and produce seedlings after fire (facultative seeders; Zedler et al. 1983; Moreno and Oechel 1991a; Beyers and Wakeman 2000; Keeley 2000). Recruitment of new genets of most seeding species is restricted primarily to the first postburn year (Keeley et al. 1981; Moreno and Oechel 1991b; Keeley 2000).

Generally, there is an abundant, but temporary, growth of herbaceous and suffrutescent vegetation in the first several years following a fire. Although short-lived, this initial growth supports high species diversity due to a profusion of postfire annuals. By the third or fourth year, shrubs dominate the site through vigorous resprouting and growth of seedlings (Sweeney 1956; Keeley 1977, 2000; Keeley and Keeley 1986). However, postfire vegetation recovery in any given location is greatly influenced by the varying means of re-establishment of the common species found on the site and in the region, by varying fire regimes (e.g., fire intensity, season,

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frequency and history), and by postburn weather patterns (Keeley et al. 1989; Moreno and Oechel 1994).

In July 2003, the lightning-ignited 9700-ha Coyote Fire swept through San Diego State University's (SDSU) Sky Oaks Field Station (San Diego County, CA), a long-term ecological research site. This study documents the impact of the Coyote Fire, specifically examining the effects of pre-fire stand age, fire intensity, and hillslope position, on patterns of vegetation recovery during the first and second postfire growing seasons in two contrasting stands of mixed chaparral at Sky Oaks. Fire intensity, the amount of heat released per unit of time, is related to fire severity, which is the effect of this heat release on ecosystem properties. A surrogate measure of fire intensity was used to analyze variations in fire severity between the two stands (Bond and van Wilgen 1996). Although chaparral responses to fire are well documented in the literature, monitoring the effects of a naturally-ignited summer wildfire at this long-term research site adds value to decades of observational and experimental studies on fire ecology that have occurred there.

Based on the literature, we expected that: (a) the abundance of fire annuals would decrease in the second postfire year, while the cover of other annuals and shrubs would increase (Keeley et al. 1981, 1985; Keeley and Keeley 1986); (b) fire intensity would be higher in the old stand due to its dense canopy and greater accumulation of fuel (Reid and Oechel 1984; Keeley 2000); (c) the diversity and abundance of herbaceous species would be higher in the young stand due a more recently replenished seed bank (Keeley et al. 1981; Keeley 2000); (d) fire intensity would decrease mature plant survival, resprouting potential, and seedling germination in most shrub species (Moreno and Oechel 1991a; Sparks and Oechel 1993); however, (e) germination of obligate seeding species would be favored by high fire intensity (Rundel et al. 1987; Borchert and Odion 1995); and, (f) patterns of pre-fire shrub densities and postfire erosion across hillslope positions would also likely impact the postfire community (Riggan et al. 1988; Davis et al. 1989; Moreno and Oechel 1991b, Rice 1993).

We addressed three main research questions: (1) Was there a difference in fire intensity between the two stands? (2) How did patterns of postfire vegetation reestablishment differ between stands in the first and second postfire year, and over time? (3) Were any other site-related factors (e.g., pre-fire shrub density, fire intensity, slope inclination, and cover of other plant groups) associated with patterns of postfire vegetation recovery?

Methods

Study Area

Sky Oaks Field Station (33° 21′ N, 116° 34′ W; 1400 m elevation) is located in northeastern San Diego County. The study includes two sites at the Field Station: (1) a young stand with a pre-burn age of 12 yr (resulting from a controlled burn in early spring of 1992), and (2) an old stand with a pre-burn age of approximately 60 yr. The prescribed burn was conducted to reduce fuel and fire hazard around micrometeorological and other instruments at the site, but, unfortunately, detailed records of that fire were lost in the 2003 Coyote fire. Prefire stand age in the old stand was determined using growth rings from three basal stem sections of the obligate seeder *Ceanothus greggii* var. *perplexans* found in an adjacent unburned patch (Keeley 1992, 1993; nomenclature follows Hickman 1993, authorities given in Table 1).

Sky Oaks was completely consumed in the Coyote Fire, which burned under hot, dry, and windy conditions. Sites were selected in an effort to minimize variability in all environmental factors except stand age. The two stands were less than 0.5 km apart, both at the same elevation and on a west-to-southwest facing slope, with slope gradients ranging between 23–29° at high hillslope positions and 9–18° at low hillslope positions. The prefire chaparral community was co-dominated by *Adenostoma fasciculatum* and *Ceanothus greggii* var. *perplexans* (Moreno and Oechel 1991a).

Mean annual precipitation at the field station is 381 mm, the majority falling between November and March (average based on unpublished data from 1994 to 2003, Sky Oaks Weather Station, SDSU Global Change Research Group). For the first precipitation year following the fire (September 2003 to August 2004), precipitation was below average, particularly in the spring of 2004. However, precipitation during the second postfire season was well above average from October 2004 through February 2005 (Fig. 1).

Data Collection

Data were collected in spring of 2004 and 2005 during the first and second post-fire growing seasons. Vegetation was sampled along three parallel 150-m transects permanently established within each stand. Transects were arranged perpendicular to the slope about 50 m apart at high-, mid- and low-hillslope positions in order to account for the effects of postfire erosion and deposition (Keeley et al. 2005a). Permanent sampling plots, each 1.0-m^2 with a 0.25-m^2 subplot, were arranged randomly within each 5-m segment of transect. This design yielded 30

TABLE 1. PLANT SPECIES FOUND IN THIS STUDY, ARRANGED BY PLANT GROUP. OS = obligate seeder; FS = facultative seeder; OR = obligate resprouter; FA = fire annual; OA = opportunistic annual; FP = fire perennial, E = exotic; Other = not assigned a group or included in analyses (because of a very low Importance Value). References for plant group designations: Keeley et al. 1981; Zedler 1981; Zedler et al. 1983; Keeley 1986; Keeley and Keeley 1986; Keeley 1991; Moreno and Oechel 1991a; Zedler 1995a; Keeley and Fotheringham 1998; Keeley 2000. Plant vouchers deposited at San Diego State University Herbarium (SDSU).

Group	Species	Family	Life form
OS	*Ceanothus greggii* A. Gray var. *perplexans* (Trel.) Jepson	Rhamnaceae	shrub
FS	*Adenostoma fasciculatum* Hook. & Arn.	Rosaceae	shrub
OR	*Adenostoma sparsifolium* Torrey	Rosaceae	shrub
	Quercus berberidifolia Liebm.	Fagaceae	shrub
FA	*Antirrhinum coulterianum* Benth.	Scrophulariaceae	herb
	Emmenanthe penduliflora Benth. var. *penduliflora*	Hydrophyllaceae	herb
	Phacelia brachyloba (Benth.) A. Gray	Hydrophyllaceae	herb
	Phacelia minor (Harvey) Thell.	Hydrophyllaceae	herb
OA	*Calyptridium monandrum* Nutt.	Portulacaceae	herb
	Camissonia hirtella (E. Greene) Raven	Onagraceae	herb
	Caulanthus heterophyllus (Nutt.) Payson var. *heterophyllus*	Brassicaceae	herb
	Chaenactis artemisiifolia (A. Gray) A. Gray	Asteraceae	herb
	Cryptantha intermedia (A. Gray) E. Greene	Boraginaceae	herb
	Cryptantha muricata (Hook. & Arn.) Nelson & J.F. Macbr.	Boraginaceae	herb
	Filago californica Nutt.	Asteraceae	herb
	Gilia australis (H. Mason & A.D. Grant) V. Grant & A.D. Grant	Polemoniaceae	herb
	Lotus strigosus (Nutt.) E. Greene	Fabaceae	herb
	Mimulus brevipes Benth.	Scrophulariaceae	herb
	Nemacladus ramosissimus Nutt.	Campanulaceae	herb
	Salvia columbariae Benth.	Lamiaceae	herb
FP	*Eriophyllum confertiflorum* (DC.) A. Gray var. *confertiflorum*	Asteraceae	suffrutescent
	Lotus scoparius (Nutt.) Ottley var. *scoparius*	Fabaceae	suffrutescent
	Penstemon centranthifolius (Benth.) Benth.	Scrophulariaceae	suffrutescent
	Penstemon spectabilis Thurber var. *spectabilis*	Scrophulariaceae	suffrutescent
	Turricula parryi (A. Gray) J.F. Macbr.	Hydrophyllaceae	suffrutescent
E	*Bromus madritensis* L. subsp. *rubens* (L.) Husnot	Poaceae	herb
	Bromus tectorum L.	Poaceae	herb
	Erodium cicutarium (L.) L'Hér.	Geraniaceae	herb
	Hordeum murinum L. subsp. *leporinum* (Link) Arcang.	Poaceae	herb
Other	*Dichelostemma capitatum* Alph. Wood subsp. *Capitatum*	Liliaceae	geophyte
	Orobanche fasciculata Nutt.	Orobanchaceae	herb
	Pellaea mucronata (D. Eaton) D. Eaton var. *mucronata*	Pteridaceae	fern
	Solanum umbelliferum Eschsch.	Solanaceae	suffrutescent
	Vulpia octoflora (Walter) Rydb. var. *octoflora*	Poaceae	herb
	Yucca whipplei Torrey	Liliaceae	suffrutescent

sampling plots per hillslope position per stand, and 90 plots per stand (see Schmalbach 2005 for details).

Measurements of herbs and shrub seedlings were made in the 0.25-m^2 sampling plots, and measurements of re-sprouting shrubs and dead stumps were made in the encompassing 1.0-m^2 plots (size based on Moreno and Oechel 1992). The number of shrub seedlings was counted, cover for each species visually estimated by two observers and averaged, and slope gradient (inclination) recorded within each plot using a clinometer. A measure of fire intensity for each sampling plot was estimated from the diameter of the smallest stem remaining on the shrub skeleton of a re-sprouting *Adenostoma fasciculatum* located nearest the center of each 1.0-m^2 plot (Moreno and Oechel 1989; Keeley et al. 2005b). Prefire shrub densities in each stand were estimated postfire using dead and resprouting stumps (Keeley et al. 2005b).

For analysis, plant species were grouped by life form, origin (native, exotic), and mode of regeneration following fire. This yielded seven functional groups: obligate seeder shrub, facultative seeder shrub, obligate resprouter shrub, fire annual, opportunistic native annual, fire perennial, and exotic annual (Table 1). For the obligate seeder and facultative seeder groups, *Ceanothus greggii* and *Adenostoma fasciculatum* (respectively) were the only shrub species recorded. Mortality of seedlings was estimated by

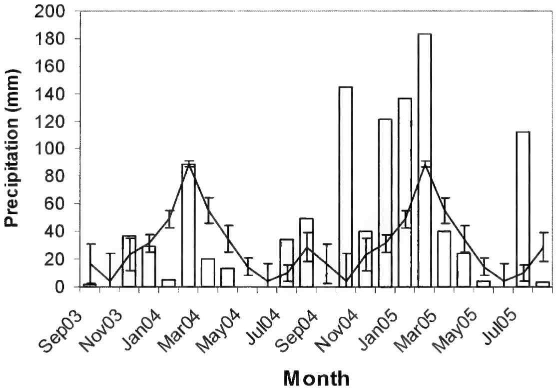

FIG. 1. Monthly precipitation at Sky Oaks Field Station for the first two precipitation years following the Coyote Fire, Sept. 2003–Aug. 2005. Line shows average precipitation per month based on the years 1994–2002. Error bars based on 1 SE. Data for Sept. and Oct. 2003 are from the Western Regional Climate Center, Oak Grove RAWS; all other data are from the Sky Oaks Weather Station.

the net change in number of seedlings from the first to second postfire year.

Data Analyses

An exploratory analysis of the data from the first postfire season (April 2004) was conducted to determine if spatial dependence was present in the dataset using spatial autocorrelation analysis (Moran's *I*; Legendre 1993; Almeida-Neto and Lewinsohn 2004). To test for differences in community recovery between the first and second postfire years, a repeated measures analysis of variance (Gurevitch and Chester 1986) was used for each plant group.

Minimum diameter was used for all analyses involving fire intensity as a factor, and it was log transformed to meet normality and heteroscedasticity assumptions. A two-sample t-test was used to determine if fire intensity differed significantly between the old and young stand. One-way ANOVAs were used to test for differences in fire intensity between hillslope positions for each stand. Two-way ANOVAs with the Bonferroni post hoc test for differences between factors were used to compare patterns of recovery between the two stands in the first and second postfire year. To incorporate the potential effects of postfire erosion and deposition, hillslope position was also included as a factor. Finally, relationships between plant group abundance and site-related variables at the plot scale were tested for significance by multiple regression analysis (backward stepwise, $P > 0.15$ to eliminate). All regressions were bootstrapped to verify their stability (statistics were calculated with SYSTAT 10.2).

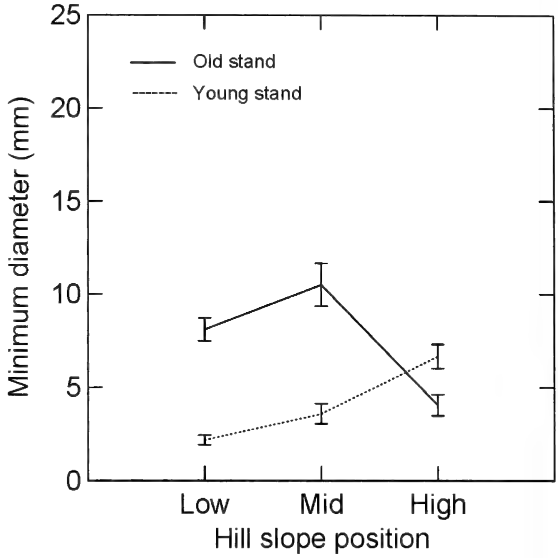

FIG. 2. Differences in fire intensity (shown as average minimum branch diameter) across hillslope positions within each stand. Error bars = 1 SE.

Due to normality and heteroscedasticity issues with both density and cover values, a relative importance value was calculated for each plant group and used in the analyses. The importance value is a weighted average of relative density, relative cover, and relative frequency (calculated per transect) for each species (Jongman et al. 1995). Importance values for each plant group were calculated by summing the relative importance values for each species within that group.

RESULTS

Spatial dependence was present only at a distance of less than or equal to 2 m ($P < 0.01$), considerably less than the average distance between sampling plots (5 m); 13% of the total sampling plots were less than or equal to 2 m apart. Consequently, observations at the sampling plots were treated as independent in all statistical analyses.

Fire Intensity

Fire intensity was significantly higher (e.g., minimum stem diameter larger) in the old stand (7 ± 5.0 mm; mean $\pm$ SD) than in the young stand (4 ± 3.3 mm; $t_{177} = 5.48$, $P < 0.001$). In the old stand, fire intensity decreased from the low to the high hillslope position. In the young stand, the pattern was opposite (Fig. 2).

Postfire Vegetation Comparisons Between Stands

First postfire year. Ceanothus greggii seedlings were significantly more abundant in the old

TABLE 2. EFFECTS OF STAND (OLD, YOUNG) AND HILLSLOPE POSITION (HIGH, MID, LOW) ON FUNCTIONAL GROUP RELATIVE ABUNDANCE (IMPORTANCE VALUE) BASED ON TWO-WAY ANOVA FOR SELECTED PLANT GROUPS IN 2004 AND 2005. F-statistics (p-value) given. (seedl = seedlings; respr = resprouts; both = seedlings + resprouts).

Factor	d.f.	OS	FS seedl	FS respr	FA	OA	E
2004							
Stand	1	492.7 (<0.001)	2.2 (0.139)	0.3 (0.582)	7.3 (0.008)	1012.9 (<0.001)	–
Hillslope	2	10.7 (<0.001)	8.1 (<0.001)	15.8 (<0.001)	4.8 (0.010)	35.5 (<0.001)	–
Stand × Hillslope	2	16.4 (<0.001)	37.7 (<0.001)	1.4 (0.245)	5.6 (0.004)	9.1 (<0.001)	–
2005							
Stand	1	519.4 (<0.001)	14.6 (<0.001)	15.6 (<0.001)	1043.4 (<0.001)	2021.1 (<0.001)	990.9 (<0.001)
Hillslope	2	20.0 (<0.001)	54.1 (<0.001)	28.0 (<0.001)	77.1 (<0.001)	628.7 (<0.001)	42.4 (<0.001)
Stand × Hillslope	2	9.1 (<0.001)	41.5 (<0.001)	0.9 (0.405)	115.4 (<0.001)	38.8 (<0.001)	11.3 (<0.001)

stand, particularly at higher hillslope positions, in the first postfire season (Table 2; Fig. 3a). The relative abundance of *Adenostoma fasciculatum*, in contrast, was most related to hillslope position (Table 2). Abundances of seedlings and resprouting shrubs did not differ significantly between stands (Fig. 3b, c). In the old stand, *A. fasciculatum* seedlings were most abundant lower or higher on the slope, while in the young stand, seedling densities increased with slope steepness (Fig. 3b). The relative abundance of *A. fasciculatum* resprouts was lowest at the low hillslope position within both stands (Fig. 3c). Densities of obligate resprouters, *Adenostoma sparsifolium* and *Quercus berberidifolia*, were too low to be analyzed (seven and three individuals, respectively).

Fire annuals (Table 1) were found in greatest abundance in the old stand primarily due to their abundance at the high hillslope position (Fig. 3d). *Phacelia brachyloba* was by far the most common fire annual species (98% of functional group density and 97% of cover in the first postfire year). Its very low abundance in the young stand at the high hillslope position appears to be the main reason for the difference between stands. Otherwise, abundance was similar across stands and hillslope positions. In contrast, opportunistic annuals (Table 1) were much more abundant in the young stand (Fig. 3e). Their relative abundance increased higher on the slope, especially in the old stand. Fire perennials (Table 1) were relatively uncommon in the first postfire year, present only as seedlings. Abundances were significantly higher in the young stand (Fig. 4), and varied with hillslope position.

Second postfire year. Relative abundances of *Ceanothus greggii* seedlings remained greatest in the old stand, and at mid hillslope positions in the second postfire year (Fig. 3a), in spite of higher seedling mortality there (noted above). In the second year, *Adenostoma fasciculatum* seedlings were slightly more abundant in the young stand and higher on the slopes (Fig. 3b).

Fire annual cover decreased dramatically in the second postfire year (Fig. 4), and *Phacelia brachyloba* became much less common than other fire annuals (its average functional group importance value decreased from 47% in 2004 to 0.2% in 2005). In the old stand, the density of fire annuals decreased by 74% and cover by 89%, and declines were even greater in the young stand (83% and 97% respectively). Abundance of fire annuals remained greatest in the old stand at the high hillslope position (Fig. 3d). Density of opportunistic native annuals, on the other hand, was 24 times greater in the second postfire year. Relative abundance remained greater in the young stand, and at high hillslope positions (Fig. 3e). The most common opportunistic annual was *Cryptantha muricata* (functional group importance value increased from zero in 2004 to 61% in 2005). Although uncommon in the first postfire year, exotic (non-native) annuals also increased significantly in the second postfire year (Fig. 4), especially low on the slope (Fig. 3f) and in the young stand.

Abundance of fire perennials increased (59%) from the first to second postfire year (Fig. 4). Two new species, *Penstemon spectabilis* and *Turricula parryi*, were recorded that had not been seen the first year. Relative abundance of fire perennials remained higher in the young stand and at high hillslope positions (not shown).

Variation in postfire recovery over time. While there was a decrease in the relative abundance of shrub seedlings in both stands between 2004 and 2005, seedling cover increased for both species (Fig. 4). *Ceanothus greggii* (obligate seeder) seedling mortality was greater in the old stand (37.1%) than in the young stand (12.1%), and differed with hillslope position within each stand (Fig. 5). Establishment of new seedlings in the second postfire year was negligible. In contrast, mortality among *Adenostoma fasciculatum* (fac-

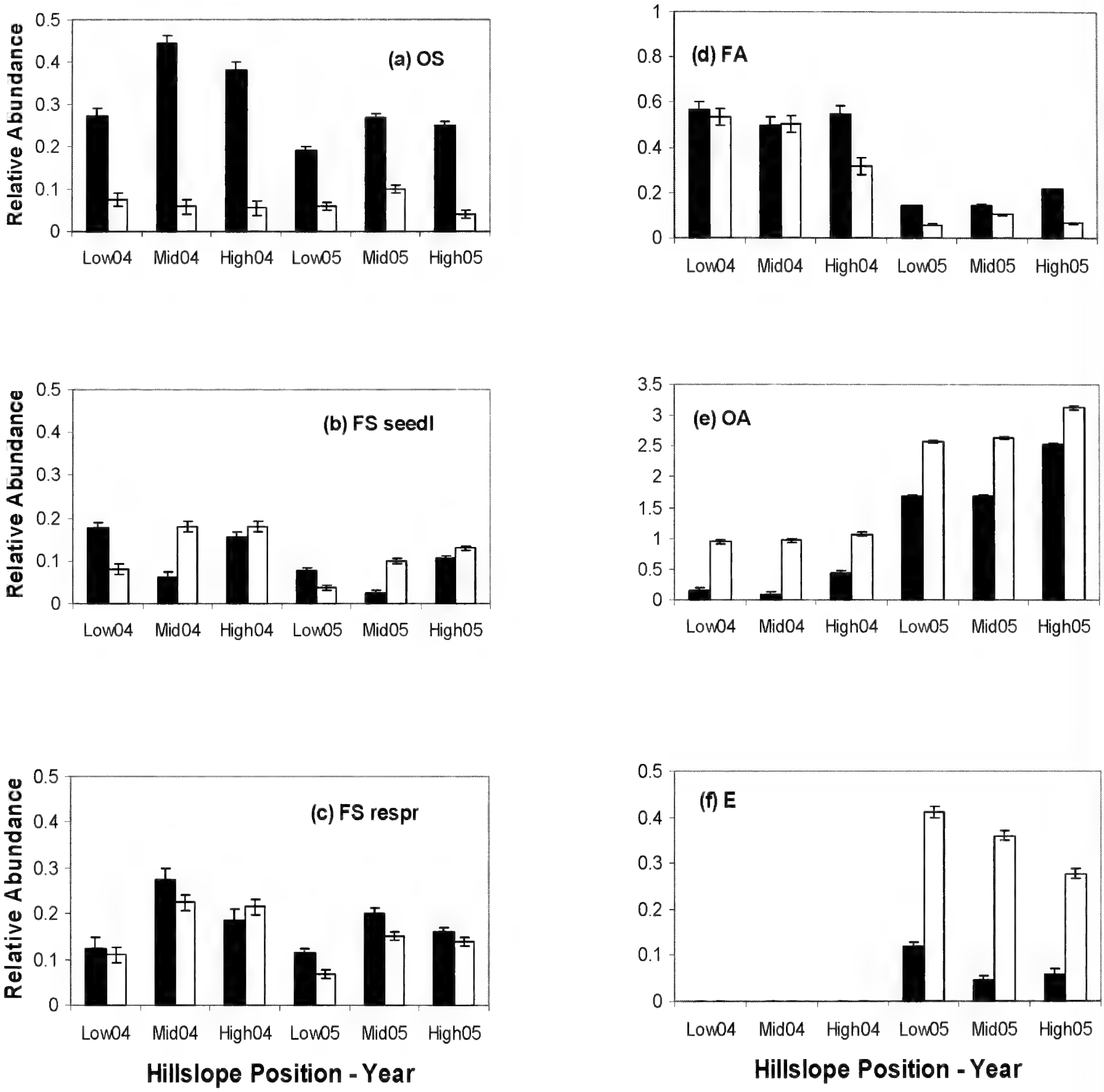

FIG. 3. Relative abundance (average importance value) of plant groups by hillslope position (Low, Mid, High) in the young and old stands for the first (04 = 2004) and second (05 = 2005): postfire seasons (black bar = old stand, white bar = young stand): (a) *C. greggii* seedlings, (b) *A. fasciculatum* seedlings, (c) *A. fasciculatum* resprouts, (d) fire annuals, (e) opportunistic annuals, and (f) exotic annuals. Note varying y-axis. Error bars = 1 SE.

ultative seeder) seedlings did not differ significantly between the two stands (Table 3), although greater mortality occurred low on the slope in both stands (Fig. 5). Cover of *A. fasciculatum* resprouts increased to the same degree in both stands and across all hillslope positions (Fig. 4); however, the relative abundance of resprouts decreased slightly in the young stand in the second postfire year as a result of other functional types increasing in abundance (Fig. 3).

The most striking difference in the herbaceous community between 2004 and 2005 was the disappearance of fire annuals in the second postfire year (Fig. 4). In contrast, there was a significant increase in the abundance of opportunistic annuals across both stands, most pronounced at the high hillslope position (Fig. 3). Exotic annuals also increased, although not as much in the old stand as in the young (Fig. 4), and in both stands abundances were highest on the low-slope position (Table 3; Fig. 3).

Spatial Patterns in Postfire Recovery at the Plot Scale

First postfire year. Data from each stand were analyzed separately given that patterns of postfire

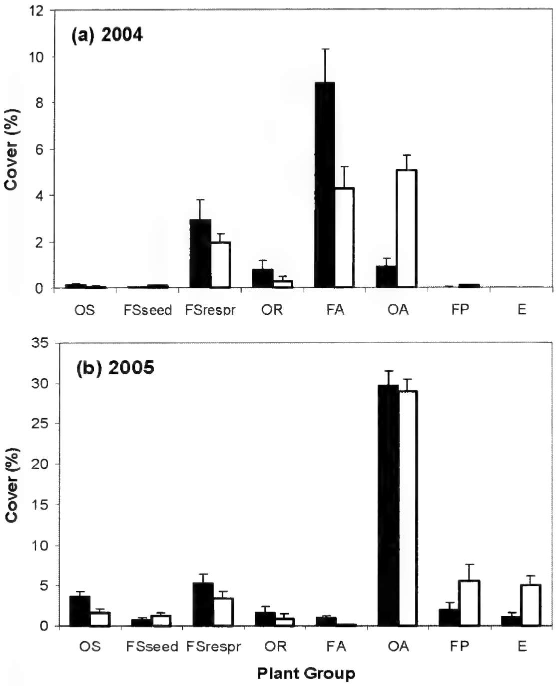

FIG. 4. Cover for each plant group by stand age (black bars = old stand, white bars = young stand) for a) first (2004), and b) second (2005) postfire year (see Table 1 for definitions of plant groups). FS group split into seedlings and resprouting shrubs. Note varying range of y-axis. Error bars = 1 SE.

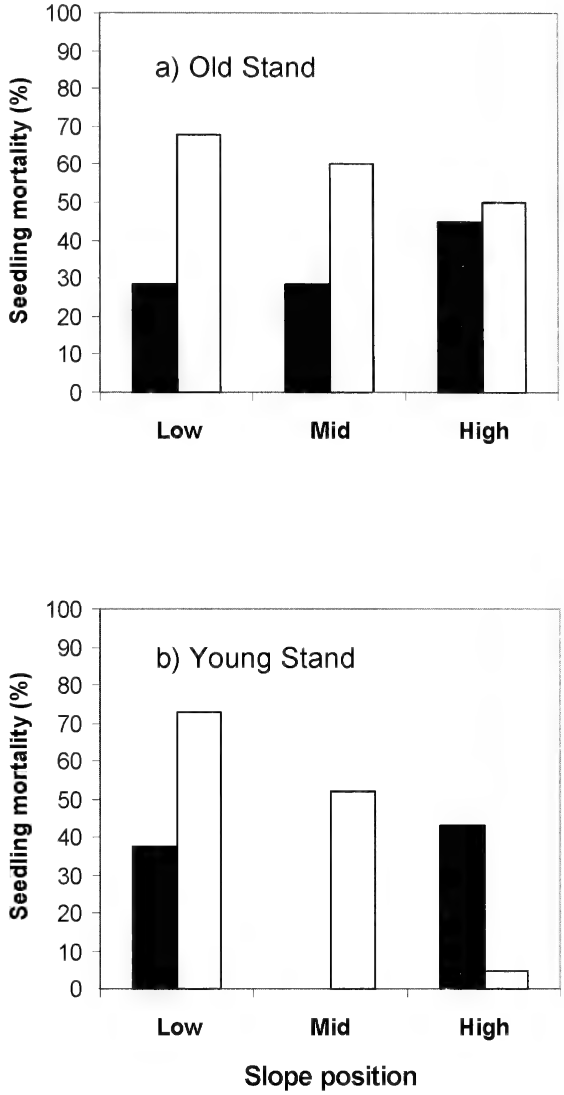

FIG. 5. Shrub seedling mortality as percent fewer individuals per hillslope position between the first and second postfire year for the (a) old stand and (b) young stand. Black bar = *Ceanothus greggii*, white bar = *Adenostoma fasciculatum*.

recovery differed between the two stands (Table 3). In the old stand, *Ceanothus greggii* (OS) seedlings were more abundant in plots on steep slopes, with higher fire intensity, and low prefire shrub densities (Table 4). In the young stand, slope was the only significant factor affecting plot-level abundance, with more seedlings found on flatter plots (which tend to occur lower on the hillslope). In contrast, more *Adenostoma fasciculatum* (FS) seedlings were found in low fire intensity areas and on flatter locations within the old stand, and where the incline was greater in the young stand (Table 4). None of the site factors

TABLE 3. EFFECTS OF YEAR (2004, 2005), STAND (OLD, YOUNG) AND HILLSLOPE POSITION (HIGH, MID, LOW) ON PLANT GROUP RELATIVE ABUNDANCE (IMPORTANCE VALUE) BASED ON REPEATED MEASURES ANOVA. F-statistics (p-values) given. Plant groups as in Table 1 (seedl = seedlings; respr = resprouts).

Factor	d.f.	OS	FS seedl	FS respr	FA	OA	E
Year	1	107.0 (<0.001)	170.0 (<0.001)	38.6 (<0.001)	594.0 (<0.001)	13300.0 (<0.001)	3370.0 (<0.001)
Year × Stand	1	116.0 (<0.001)	0.3 (0.611)	2.8 (0.094)	0.1 (0.806)	2.7 (0.102)	1390.0 (<0.001)
Year × Hillslope	2	1.6 (0.208)	1.7 (0.191)	2.8 (0.064)	9.1 (<0.001)	104.0 (<0.001)	58.8 (<0.001)
Year × Stand × Hillslope	2	12.5 (<0.001)	10.1 (<0.001)	0.8 (0.438)	2.1 (0.123)	2.0 (0.142)	10.9 (<0.001)

TABLE 4. REGRESSION ANALYSIS OF IMPORTANCE VALUES OF PLANT GROUPS (AS IN TABLE 1) VS. SITE PARAMETERS FOR: A) THE FIRST AND B) SECOND POSTFIRE YEARS. Shown is the t-value/coefficient for each factor if $P < 0.05$; *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$; $n = 90$.

a)	Year 1				
Variable	OS old	OS young	FS old	FS young	FA young
Slope	2.949/0.010**	−2.277/−0.002*	−2.497/−0.005*	5.294/0.008***	−3.544/−0.013***
Fire intensity	2.800/0.164**		−3.474/−0.112***		
Shrub density	−2.213/−0.079*				−2.093/−0.121*
OA cover					−2.341/−0.007*

b)	Year 2				
Variable	OS young	OA old	OA young	E old	E young
Slope		8.646/0.057***	9.040/0.031***	−3.120/−0.003**	−2.020/−0.004*
Fire intensity		−3.572/−0.403***	2.830/0.225**		−3.033/−0.114
Shrub density			−3.230/−0.165**	2.619/0.039*	
OA cover	−2.968/−0.001**				−2.434/−0.002*
OS cover		−2.550/−0.012*	−2.796/−0.009**		
FP cover			−3.942/−0.004***		
E cover			−4.252/−0.006***		
FS cover				−2.113/−0.001*	

significantly affected the distribution of fire annuals in the old stand, while their cover was negatively related to slope, prefire shrub density and cover of opportunistic annuals in the young stand.

Second postfire year. In the young stand, abundance of *Ceanothus greggii* seedlings was negatively related to dense cover of opportunistic annuals in the second year (Table 4). Prefire shrub density and/or cover of other functional groups was negatively correlated with the abundance of opportunistic annuals (OA) in the young stand. The effect of fire intensity on OA was negative in the old stand, but positive in the young, but probably because OA were abundant at high hillslope position (Fig. 3e) where fire intensity differed between stands (Fig. 2). In the old stand, exotics were found in greater abundance on flatter plots where cover of facultative seeder resprouts was less and prefire shrub densities greater. Abundances in the young stand were also greatest on flatter areas where the cover of other annuals was sparse and fire intensity was low (Table 4).

DISCUSSION

Different fire regimes and fire characteristics tend to favor particular plant species based on their mode of regeneration following a fire, and by doing so affect patterns of postfire community composition (Haidinger and Keeley 1993). Variations in soil heating, in particular, can greatly affect recruitment because seeds have different tolerances to heat and different requirements for germination (Keeley and Keeley 1981; Keeley et al. 1985; Zammit and Zedler 1988; Zedler 1995a; Odion and Davis 2000; Le Fer and Parker 2005). Consequently, postfire recovery patterns among different plant groups are likely to be strongly influenced by fire intensity, and other factors affected by stand age (Moreno and Oechel 1994; Tyler 1995). We found important differences in regeneration patterns between the old and the young stand among the various plant groups.

Fire intensity during the Coyote Fire was higher in the old stand, corresponding to a difference in pre-fire shrub densities, which were also higher in the old stand. Fire intensity was negatively correlated with hillslope position in the old stand, but positively in the young stand. These patterns did not correspond to differences in prefire shrub densities among hillslope positions and may be related to variations in fire behavior or the pattern of burning during the 2003 Coyote Fire, which are unknown.

Mature obligate seeders (e.g., *Ceanothus greggii*) are killed by fire, and recovery of the population depends on the fire-cued germination of seed that have accumulated in the soil over time (Keeley and Zedler 1978; Zedler 1981). Although it has been hypothesized that seed banks may diminish in mature stands of chaparral, there is little evidence of seed bank decline in stands younger than 80-years of age (Keeley 1977; Zammit and Zedler 1988, 1992; Keeley et al. 1989). The old stand at Sky Oaks was estimated to be approximately 60-years old prior to the Coyote Fire, and sustained a mass recruitment of *C. greggii* seedlings in the first postfire season (12.4 ± 1.6 m^{-2}; mean $\pm$ SD). Seedling recruitment was lower (1.6 ± 0.5 m^{-2}) in the young stand (12-years old), suggesting that *C. greggii* — which requires up to 25 yr to replenish its seed bank (Keeley 1986) — did not accumulate as large a seed bank in this stand during the shorter interval between fires. Further, fire in-

tensity during the 1992 prescribed fire and/or the 2003 Coyote Fire may not have been sufficient to stimulate much germination in this stand (Le Fer and Parker 2005).

In contrast, *Adenostoma fasciculatum* both resprouts and reestablishes from fire-cued germination following a burn, and is generally more resilient to recurrent fires in terms of seedling recruitment (Zedler 1981, 1995b; Moreno and Oechel 1993). Our data are consistent with this in that the abundance of *A. fasciculatum* seedlings did not differ significantly between stands in the first postfire year (old stand = 2.6 ± 0.7 m^{-2}, mean $\pm$ SD; young stand = 2.7 ± 0.5 m^{-2}). As also found in previous studies, however, fire intensity had a significant effect on patterns of establishment (Moreno and Oechel 1991a; Davis et al. 1989). *Adenostoma fasciculatum* seedlings were more abundant in areas with less intense fire, while *C. greggii* abundance was positively correlated with fire intensity.

Seedlings of both species suffered significant mortality between the first and second postfire years. Previous research has found that seedling mortality is strongly related to soil moisture levels during the first six months following germination (Moreno and Oechel 1992). *Ceanothus greggii* mortality was greatest at the high hillslope positions within each stand, where soil moisture levels were probably lower due to steep inclines (Meentemeyer et al. 2001). *Adenostoma fasciculatum* seedlings did not suffer greater mortality at high hillslope positions, however, even though these seedlings have been found to be more sensitive to drying of the soil than *C. greggii* seedlings (Moreno and Oechel 1988, 1992). Herbivory by small mammals is also an important source of mortality and can greatly affect patterns of seedling establishment in the postfire community (Mills 1986; Mills and Kummerow 1989). Overall, *C. greggii* seedlings had a higher rate of survival overall than *A. fasciculatum* seedlings. Recruitment of new seedlings in the second year was negligible, most likely due to a lack of second year germination and/or increased competition from resprouters and already established plants (Keeley 2000; Quintana et al. 2004).

There was no evidence that high fire intensity, over the range of values observed, negatively affected resprouting success in the first postfire year, as has been reported in other studies (Malanson and O'Leary 1985; Rundel et al. 1987; Moreno and Oechel 1991b; Borchert and Odion 1995). Resprout cover increased in the second postfire year in both stands and across all hillslope positions. However, the density and frequency of *A. fasciculatum* resprouts decreased in the young stand between the first and second postfire years. One possible explanation is that energy reserves for resprouting in the young stand, when compared to the old stand, were reduced by the prescribed burn in 1992 and as a result were insufficient to support some of the resprouting shrubs through the second postfire year (Moreno and Oechel 1991b, 1993).

Fire annuals were the most conspicuous herbaceous component of the burn area in the first postfire season, and then virtually disappeared from the landscape in the second year. They arise from a dormant seedbank that is only stimulated to germinate by charred wood, smoke, or heat shock (Keeley et al. 1981, 1985; Keeley and Keeley 1986; Moreno and Oechel 1991a). Contrary to expectations, fire annuals were found in greater abundance in the old stand, where fire intensity was greater, than in the young stand where the prescribed fire that took place 12 years prior to the Coyote Fire was expected to have replenished the seed bank (Keeley et al. 1981; Keeley 2000). Lower germination of fire annuals in the young stand may have resulted from: a) seed bank depletion due to reduced fire intensity during the 1992 controlled burn, reducing the density of seed available for germination after the 2003 fire; b) reduced fire intensity during the 2003 fire, which failed to stimulate germination; and/or c) greater mortality of seeds under moist soil conditions, such as those perhaps present during the spring-time controlled burn in 1992 (Beadle 1940; Sweeney 1956; Le Fer and Parker 2005). Postfire erosion following the 1992 and/or 2003 fires may further explain why fire annuals were least abundant at the high hillslope position in the young stand.

Opportunistic annuals occur in openings in mature chaparral and are common in the early postfire seasons (Keeley et al. 2005a). They have a polymorphic seed bank that contains both nonrefractory (opportunistic) and refractory (enhanced germination after fire) seeds (Keeley et al. 1981). While fire annuals were more abundant in the old stand in the first postfire year, opportunistic annuals were more abundant in the young stand where fire intensity was lower. Other studies have also found a negative relationship between the abundance of herbaceous species and fire intensity (Moreno and Oechel 1991a; Keeley 2000). The abundance of opportunistic annuals increased dramatically in the second postfire season, making up 88% of the total herbaceous cover in the old stand, and 73% in the young stand. This was also a year with above average precipitation.

Herbs are generally absent beneath the mature chaparral canopy, but common as seedlings after fire through the enhanced fire-cued germination of soil-stored seed (Keeley et al. 1981; Keeley 2000). Fire perennials were found in greatest abundance in the young stand, perhaps because fire intensity was lower, or because mature plants were still present in the community following the

1992 prescribed burn (Keeley et al. 1981; Keeley 2000).

Seeds of exotic annuals have low residence time in the soil, thus the presence of these species on burn sites is primarily due to postburn colonization. Most, such as species of *Bromus* and *Erodium*, disperse prior to the summer fire season. As a result, they are less common in the first postfire year but present in subsequent years (Keeley 2000), as was seen at Sky Oaks after the Coyote Fire. Exotics were found in significantly greater abundance in the young stand. However, this could be a result of the proximity of the young stand to the field station office area and instrument sites — an area of high human traffic — rather than a consequence of stand age. Abundances were also highest at the low hillslope positions within each stand, and then decreased farther up hill. This pattern may indicate that exotics are dispersing from the office area and access road (which runs along the base of the slope).

Summary

In general, postfire succession in the two mixed chaparral stands at Sky Oaks has been following the general model of chaparral succession as described by other investigators (Horton and Kraebel 1955; Sweeney 1956; Hanes 1971; Keeley 1977; Keeley et al. 1981; Keeley 2000). However, the fire history of a specific site also creates a "legacy effect" (Foster et al. 1998), resulting from the interval, season, and behavior (e.g., prescribed vs. natural; Le Fer and Parker 2005) of the previous fires, which can affect patterns of postfire recovery through future fire cycles. This may have management implications for spring burning in chaparral. Our finding of significantly lower abundance of fire annuals in the young stand illustrates the potentially negative impact to postfire species diversity that may result from reduced fire intensity and altered germination behavior following spring burning.

Based on our findings, the following can be concluded regarding the patterns of postfire vegetation recovery in the two stands at Sky Oaks:

(1) As expected, fire intensity was significantly greater in the older chaparral stand. Variation in fire intensity significantly affected patterns of postfire regeneration in several plant groups.

(2) There were significant differences between stands in the patterns of reestablishment for all plant groups during the first and/or second postfire year. Many differences were as predicted given the relative age of, and fire intensity differences between, the stands.

(3) Other site-related variables, however, were also associated with patterns of postfire vegetation reestablishment, in particular hillslope position and prefire shrub density. The effects of hillslope position suggest that factors such as prefire species patterns, soil moisture, nutrient dynamics, and erosion and deposition play a role in the postfire patterns of most plant groups. Spatial patterns found in the abundance of each plant group in relation to changes in prefire shrub density imply that a landscape of different-aged stands burning at varying intervals may lead to enhanced biodiversity in chaparral.

Our ability to infer the causes of the observed patterns is limited by the lack of spatial replication, but this is a common problem in disturbance ecology (there was only one Coyote Fire, and only one southwest-facing hillslope at Sky Oaks). However, the future value of this study may lie in continued monitoring at this permanent research site, which could complement extensive regional surveys (e.g., Keeley et al. 2005a). In particular, we predict that the abundance of exotic herbaceous species will decline as the shrub canopy closes at the field station. This may also serve as an important reference site for comparison with the very large area of southern California that burned a few months later in the October 2003 fire storm, much of that area in the wildland-urban interface (Moritz et al. 2004).

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RESPONSE TO FIRE OF *CEANOTHUS RODERICKII* (RHAMNACEAE), A FEDERALLY ENDANGERED CALIFORNIA ENDEMIC SHRUB

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ABSTRACT

Experimental burns involving rare plants can provide important information for managers of those species. This study examined the response to prescribed fire of *Ceanothus roderickii*, a federally endangered chaparral species endemic to gabbro soils of the Pine Hill Formation in western El Dorado County, California. I conducted a laboratory study of germination cues, a field comparison of germination and survival on burned and unburned plots, and a comparison of seedling survival in burned plot subplots that were protected from vertebrate herbivores by wire exclosures. Seed germination was stimulated by heat (70° or 100° C) followed by a cold treatment. Burned plots contained 22-fold more seedlings than unburned plots, and seedling survival was significantly greater on burned plots. Exclosures significantly increased seedling survival on burned plots by 2 yr postfire. Plants on burned plots began to bloom and to branch layer (root at the nodes) by the sixth year postfire, with larger plants producing more fruits and being more likely to branch layer. I concluded that *C. roderickii* was similar to other species in the subgenus *Cerastes* in its obligate-seeding response to fire. However, its ability to branch layer enabled *C. roderickii* to increase plant density in burned plots, and thus continue postfire population recovery, long after fire-stimulated seedling establishment ceased. Branch layering by *C. roderickii* allows a postfire recovery pathway that is unique among species of obligate seeding *Ceanothus* studied to date.

Key Words: *Ceanothus*, chaparral, demography, endangered species, fire, gabbro, Pine Hill Formation.

Geology has a very important influence on plants (Kruckeberg 2002). In the western foothills of the central portion of California's Sierra Nevada, a small (104 km^2) area of soils derived from a gabbro intrusion (the Pine Hill Formation) in western El Dorado County hosts a number of plants with limited or disjunct distributions (Hunter and Horenstein 1991; U.S. Fish and Wildlife Service 2002). Four of these are endemic to this formation: *Ceanothus roderickii* Knight; *Fremontodendron californicum* (Torrey) Cov. subsp. *decumbens* (R. Lloyd) Munz; *Galium californicum* Hook. & Arn. subsp. *sierrae* Dempster & Stebb.; and *Wyethia reticulata* E. Greene (Hunter and Horenstein 1991; U.S. Fish and Wildlife Service 2002). The restricted ranges of these species, along with rapid development of the area, have resulted in all but *W. reticulata* being listed as federally endangered (U.S. Fish and Wildlife Service 1996). All these species have populations growing on the Pine Hill Ecological Preserve, a 97 ha area established in 1979 to help protect these endangered species (U.S. Fish and Wildlife Service 2002).

Ceanothus roderickii was described by Knight (1968) as a prostrate or almost prostrate shrub in the subgenus *Cerastes*. It has suberect leaves and produces bluish-tinged flowers in late spring (Hickman 1993; U.S. Fish and Wildlife Service 2002). Fross and Wilken (2006) consider it closely related to (and perhaps part of) *C. cuneatus*, a widespread species containing considerable variation. Knight (1968) mentioned that the prostrate branches of *C. roderickii* radiate from a central point (reminiscent of a wagon wheel) and that the branches tend to "arch" and root at the contact point of the arch. Thus, the shrub has a sprawling habit and can proliferate its rooting points through branch layering (rooting of branches). Of all California taxa of *Ceanothus*, Hickman (1993) reports only five others that root at the nodes, viz.: *C. confusus* J. Howell, *C. fresnensis* Abrams, *C. pinetorum* Cov., *C. prostratus* Benth., and *C. pumilus* E. Greene. To my knowledge the response to fire of these node-rooting species has not been studied.

As with many rare plant species, little ecological information is available for *C. roderickii* (U.S. Fish and Wildlife Service 1996). Thus, managers are hampered in their efforts to care for protected populations because this lack of information may prevent them from taking management actions for which the effects on the species are unknown. For example, the federally endangered maritime chaparral shrub *Arctostaphylos morroensis* Weisl. & Schreiber (Ericaceae) requires fire to stimulate seed germination but adult shrubs are killed by fire; prescribed fire may increase or decrease population size depending on the extent of seedling establishment (Odion and

Tyler 2002). Consequently, managers seeking to stimulate recruitment of this species via application of prescribed fire are gambling that adequate seedling establishment will occur to allow burned populations to recover. *Ceanothus roderickii* grows in openings in chaparral vegetation on the Pine Hill Formation (U.S. Fish and Wildlife Service 2002). Chaparral is a fire-adapted community and its plants possess various adaptations to fire (Keeley and Keeley 1988) but, prior to this study, the response to fire of *C. roderickii* was unknown.

In general, the post-fire response of chaparral shrubs differs between obligate seeders and sprouters (Keeley and Zedler 1978; Keeley and Keeley 1988). In obligate seeder species, shrubs are killed by fire and the population recovers via fire-stimulated recruitment from the seed bank. In sprouter species, shrubs resprout postfire and, for some species (i.e., facultative sprouters), additional individuals may be recruited from a persistent seed bank. The subgenus *Cerastes* of *Ceanothus* (to which *C. roderickii* belongs) contains obligate seeders and thus postfire population recovery of *C. roderickii* is expected to be similar to that of other species in this section. Typically, dense postfire seedling recruitment is modified by great mortality during establishment and thinning stages to result in a mature stand of plants about two decades postfire (e.g., Schlesinger et al. 1982). However, rooting of branches (branch layering), such as occurs for *C. roderickii,* may aid in postfire population recovery. Instead of a decline in density over time due to mortality of seedlings produced postfire, as has been shown for several obligate seeding *Ceanothus* species (e.g. Schlesinger et al. 1982; Zammit and Zedler 1993), *C. roderickii* populations may be able to increase density by branch layering when plants reach suitable size. However, the recent monograph on the genus by Fross and Wilken (2006) reports this species as "…reproducing entirely from seeds." The contribution of branch layering to postfire population recovery is thus in need of study.

Herbivory can greatly impact postfire growth and survival of chaparral plants (Davis 1967), including *Ceanothus* species (e.g., Bullock 1991). For example, Mills (1986) found that seedlings protected by exclosures had significantly greater survival and growth rates than those exposed to mammalian herbivores. He also reported that mammalian herbivores damaged seedlings differentially among shrub species: seedlings of *Ceanothus greggii* A. Gray were impacted by mammalian herbivory to a greater extent than those of chamise (*Adenostoma fasciculatum* Hook. & Arn). Thus, mammalian herbivore activity may be a factor important in postfire recovery of rare chaparral shrubs (such as *C. roderickii*) and deserves experimental assessment.

This study was designed to generate information regarding the effects of fire on *C. roderickii.* Its specific objectives were to determine: 1) if seed germination is stimulated by fire (using both lab and field studies); 2) if mature plants survive fire in the field; 3) some important demographic features of postfire recovery (plant size distributions, time to sexual maturity, time to rooting by the prostrate branches); and 4) the importance of mammalian herbivory to postfire population recovery.

Methods

Study Site

This study was conducted at the Pine Hill Ecological Reserve, a conservation unit managed by the California Department of Fish and Game and centered on Pine Hill (elevation 628 m; 38°43′ lat., 120°00′ long.) in western El Dorado County, California. An area of about 1 ha along the top of the rocky ridge to the west of the summit was designated for a prescribed fire in the fall of 1984 (Boyd 2001). The burn was designed to test the responses to fire of three rare plant species found in this ecological reserve: *C. roderickii, Fremontodendron californicum* subsp. *decumbens* and *Wyethia reticulata.* Patches of *C. roderickii* were found in the open chaparral on the south-facing slope of this area. Plants were located in small open areas between shrubs and under shrub canopies (mainly *Arctostaphylos viscida* Parry with some *Adenostoma fasciculatum*).

Laboratory Germination Study

Seeds were collected in late June 1986 from dehiscing capsules produced by plants in unburned chaparral adjacent to the burn site. Because seeds of this federally endangered species were limited in quantity, this experiment examined the effects of heat and cold treatments sequentially rather than as independent factors. Fully formed, dark seeds were divided into three groups of forty seeds each. One group was not treated, the second was placed for 5 min in a forced convection oven heated to 70°C, and the third group was placed for 5 min into the oven heated to 100°C. Seeds from each treatment were divided into groups of ten seeds and each group was placed into a small (5 cm diameter) plastic Petri plate on a piece of filter paper moistened with de-ionized water. Petri plates were placed into a dark drawer kept at room temperature for 2 mo, at the end of which time any germination was noted. They then were placed into a coldroom (5°C) for 3 moths, after which they were removed and placed at room temperature for 2 wk. The number of germinating seeds (defined as emer-

gence of the radicle from the seed coat) was counted during that time. Effects of temperature treatments on germination were analyzed by Analysis of Variance (ANOVA) after log transformation of germinating seed numbers so that these count data would better meet the assumptions behind ANOVA (Zar 1996). Fisher's Probable Least Significant Difference (PLSD) test was used to compare means between temperature treatments (Abacus Concepts 1998).

Experimental Field Plots

All plots were located on the south-facing slope of the ridge upon which the prescribed fire was to be conducted. I selected nine 2 × 2 m plots with a relatively high cover of *Ceanothus roderickii* within the burn area, and nine similar plots outside the burn area, marking the corners of each with metal stakes. Plots were selected so that burned and unburned plots contained approximately similar densities of *C. roderickii.* To test this, I counted the number of rooting points (defined as a relatively discrete area of rooted branches) in each plot and compared the counts using a Mann-Whitney U test (Abacus Concepts 1998).

Most of the plots that had high *C. roderickii* cover in the burn area contained little fuel because the chaparral in that area had been cut in 1969 (Stebbins 1979) and had not recovered enough biomass to carry a fire. In order to apply fire uniformly to these plots, drying branches from shrubs cut during firebreak establishment were placed on these plots to a depth of about 0.75 m.

Maximum temperatures on the plots during burning were measured using temperature indicators made from temperature-indicating crayons (Omega Engineering, Stamford, CT). Melting points of the crayons used were 39, 59, 79, 87, 121, 142, 163, 184, 198, 226, 246, 288, 329, 343, 454, 550, 649, 760, 871, 982, 1090 and 1316°C. Temperature intervals between melting points of these crayons were approximately 20°C apart below 343°C and 110°C above. Each crayon was cut into small chips and one chip from each crayon was placed into an 8 × 4.5 cm envelope made of 1.4 mm-mesh steel screen. One of these temperature indicators was placed on the soil surface in the center of each burn plot before cut brush was piled onto the plots. Plots were burned 27 October 1983 (Boyd 2001). Conditions on the burn site were: relative humidity 36%, wind 0–6 kph and fuel moisture (measured with a 10-hr fuel stick) 7%. Temperature indicators were collected after the fire and the unmelted crayon pieces were used to determine the maximum soil surface temperature during the burning of each plot.

Response to Fire

Germination of *C. roderickii* in the burned plots was observed during the winter and spring of 1984. When emergence of new seedlings had slowed markedly (23 March 1984), I counted seedlings on each burned and unburned plot and, by periodic re-counting, followed their survival over the next two years. Plots were revisited at about monthly intervals until December 1984, every 1–2 mos during the winter and spring of 1985, once each in summer and fall of 1985, and once in the spring of 1986. The number of live plants from the 1984 cohort was counted each time, and during the late springs of 1985 and 1986 counts were made of additional seedlings in each plot that had germinated during the winter and spring of those years. Seedlings in burned plots that germinated in herbivore exclosure subplots (see description below) were excluded from this dataset. The few seedlings found in 1985 were marked with small bamboo stakes to allow their survival to be tracked independently from the 1984 cohort.

Surviving plants were measured during the second (1985) and sixth (1989) growing seasons after the fire to document the size structure of the population as well as to note the timing and extent of fruiting and branch layering. On 20 May 1985, 423 d after seedlings were first counted, I measured the size of each surviving plant in each burned plot. The length and width of each plant's canopy, measured as the longest dimension (length) and then the measurement of the canopy taken at right angles to the length (width), were recorded as well as the maximum height of the plant measured perpendicularly to the ground. These measurements were converted into canopy volumes (Boyd and Serafini 1992) using the formula for the height of a cylinder ($V = L \times W \times H \times \pi/4$). Four years later (17 June 1989), at the end of the sixth spring after the fire and 1913 d after seedlings were first counted, I revisited the burned plots and again measured the size of each surviving plant. In addition, for each plant I noted the number of mature fruits produced, whether any branches had rooted, and the distance from each crown to the rooting points of those branches. Plants in herbivore exclosures (see below) were excluded from these measurements.

Herbivore Exclosure Study

Wire mesh exclosures made of 5-mm mesh hardware cloth were used to exclude vertebrate herbivores from subplots in the burned plots. Exclosures were 25 cm long, 29 cm wide and 10 cm tall. Exclosed plots were matched with open plots of equal size by the following procedure. Two diagonal lines were established to

TABLE 1. COMPARISON OF PRE-FIRE ROOTING POINT AND POST-FIRE SEEDLING DENSITIES ON BURNED AND UNBURNED PLOTS. Data are means (SE), n = 9. P-values are the results of Mann-Whitney U tests comparing data from burned and unburned plots.

Parameter	Burned plots	Unburned plots	P-value
Rooting points (per m^2)	15.5 (1.7)	14.3 (1.0)	0.72
First year seedlings (per m^2)			
1984	24 (9.3)	1.1 (0.33)	0.0003
1985	0.25 (0.093)	1.1 (0.35)	0.052
1986	0.11 (0.085)	1.55 (0.53)	0.003

connect opposite corner markers of each plot. On the north side of each plot, one location along each diagonal line 40 cm from the corner marker was marked. If a location would make a poor experimental plot due to the presence of a large rock at the soil surface, the location was moved along the diagonal line until an area of exposed soil of suitable size was found. Once a pair of locations was marked, I flipped a coin to determine which would be covered by an exclosure and which would not. Exclosures were anchored to the ground by small (4 mm dia.) bamboo skewers and the corners of corresponding open plots (the areas of which were equal to those of exclosed plots) also were marked by bamboo skewers. A similar procedure was used to establish a pair of subplots (one exclosed and one open) on the south side of each plot. Subplots were established on 7 February 1984.

Seedlings were counted on 23 March 1984, after germination of *C. roderickii* had apparently ceased, and seedlings were recounted at approximately monthly intervals until December 1984. Afterward, I counted them at more sporadic intervals until 25 April 1986, more than two years from the start of seedling counts. Survival of seedlings in exclosures was compared to survival of seedlings in unexclosed plots using survival analysis (Abacus Concepts 1998), utilizing the Kaplan-Meier estimate with treatment significance determined by the Peto-Peto-Wilcoxon test at $\alpha \leq 0.05$ (Abacus Concepts 1998).

RESULTS

Laboratory Germination Study

Germination did not occur until seeds had been stratified. Seeds failed to germinate following the heat treatments after remaining for 2 mo at room temperature. However, after the cold treatment, seeds that had been heat-treated germinated rapidly (during 2 wk) and to similar extents. There was a significant temperature treatment effect (ANOVA; $F_{2,9} = 42$, $P < 0.0001$) because seeds that were not heat-treated did not germinate, even after stratification. Mean germination by seeds heated to 70°C was 38 ± 2.5% (SE) whereas germination by those heated to 100°C was 53 ± 14% (SE); these heat treatment means were not significantly different (Fisher's PLSD test; P = 0.38).

Response to Fire

Burned and unburned plots had statistically equal densities of *C. roderickii* prior to burning, with mean densities of approximately 15 rooting points m^{-2} (Table 1). Maximum temperatures recorded at the soil surface in burned plots were 980°–1316°C, with seven plots reaching 1090°C. All of the *C. roderickii* plants in burned plots were killed by fire.

Seedlings of *C. roderickii* occurred in both burned and unburned plots during 1984–1986. During the winter and spring of 1984, many seedlings (858) germinated on the burned plots and some (39) were found on unburned plots (Table 1). During the following two years, however, more seedlings were counted on unburned plots than on burned plots. Burned plots produced few seedlings after the initial flush of germinants in 1984 (Table 1). In 1985, unburned plots had 4-fold greater seedling density (Table 1), although this was only marginally statistically significant from seedling density on burned plots. In 1986, this difference increased and unburned plots contained significantly greater (14-fold higher) seedling density than burned plots (Table 1).

Survival of seedlings appearing on burned plots in 1984 was significantly greater than for seedlings germinating on unburned plots (Fig. 1; Peto-Peto-Wilcoxon rank test, P < 0.0001). Many seedlings in both types of plots appeared to have died from drought during late spring and early summer 1984 (judging by their wilted and shriveled appearance), whereas I noted vertebrate herbivore damage to some burned plot seedlings during June and July of 1984 and at some later census intervals. By 20 September 1984 (181 d after seedling monitoring began), only a single seedling remained alive in all unburned plots whereas burned plots contained a mean of 30 ± 13 (SE) seedlings. Some additional mortality also occurred in the burned plots after 20 September 1984 (Fig. 1). By April 1986 (763 d), 19% of plants on burned plots remained alive (Fig. 1) and by June 1989 (after 1913 d or 5.2 yr) 12% of plants on burned plots were alive.

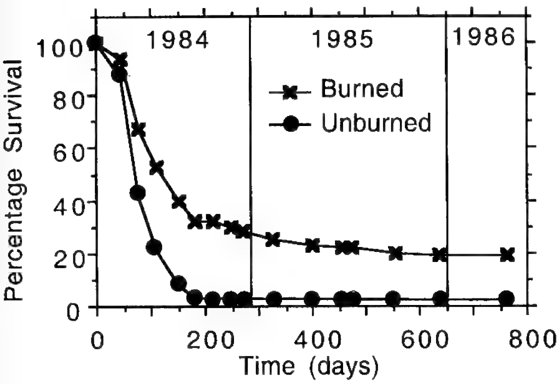

FIG. 1. Survival of seedlings on burned and unburned plots from 23 March 1984 until 25 April 1986. Time in days is measured from 23 March 1984, at which time 858 seedlings were counted on burned plots and 39 on unburned plots.

Within the burned plots, 98.5% of all seedlings found during 1984–1986 germinated the first season postfire (1984). Seedling survival on burned plots varied greatly among plots. Despite all burned plots having roughly similar numbers of rooting points prefire (range 32–91), by 1989 two plots had only one surviving plant and another had just two. Many (64, or 66%) of the 97 plants surviving in 1989 were concentrated in just two of the burned plots. There was little correlation between the prefire count of rooting points and the number of plants counted on burned plots in 1989 (simple linear regression, $r^2 = 0.034$): for example, the plot with the greatest prefire count of rooting points (91) contained just two plants in 1989.

Plants on burned plots in May 1985 were relatively small (Fig. 2), but the single unburned plot plant still alive from the 1984 cohort was 0.001 dm^3 in volume and equaled some of the smallest of the burned plot seedlings. Plants in burned plots had grown rapidly by 1989 (Fig. 2) so that mean plant size (11 ± 1.3 dm^3 [mean $\pm$ 1 SE]) was 145-fold that of plants measured in May 1985 (0.076 ± 0.0078 dm^3).

One plant in the burned plots fruited in 1988. In 1989 (six seasons post-fire), many plants on the burned plots (33%) produced at least one fruit. Fruit production per plot in 1989 varied widely (0–280) and there was a strong positive relationship between number of plants per plot and fruit production per plot (linear regression; $F_{1,7} = 34$, $P = 0.0006$, $r^2 = 0.81$). For convenience, I arbitrarily divided 1989 plants into five size classes (0–10, 10–20, 20–30, 30–40, and > 40 dm^3) to investigate the influence of plant size on fruiting and branch layering. The proportion of individuals fruiting varied significantly with plant size (contingency table analysis; $\chi^2 = 26$, df $= 4$, $P < 0.0001$) and fruiting was concentrated among the larger size classes of

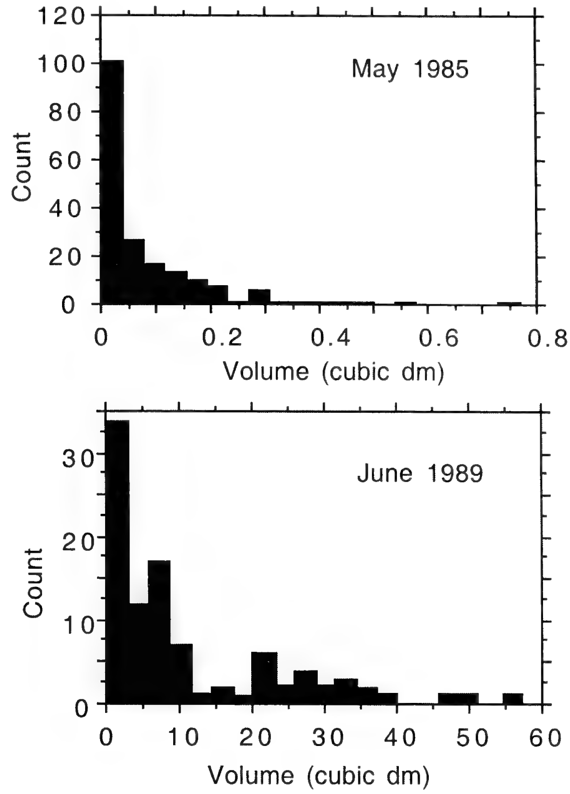

FIG. 2. Size distributions of plants (in dm^3) on burned plots in May 1985 (during the second growing season postfire) and June 1989 (during the sixth season postfire).

plants (Table 2). Only 19% of the many relatively small plants (< 10 dm^3) produced fruits, whereas at least 38% of the plants in the larger size classes produced fruits (Table 2). The number of fruits produced by each plant also increased significantly with plant size (linear regression; $F_{1,95} = 14$, $P = 0.0003$), although the relationship was rather weak ($r^2 = 0.13$).

Rooting of the longer branches of some plants was observed in 1989. At that time, 23% of the 97 plants surviving outside of exclosures had pro-

TABLE 2. DISTRIBUTION OF FRUITING INDIVIDUALS AND THOSE PRODUCING ROOTED BRANCHES AMONG THE SIZE CLASSES (DIVIDED BY CANOPY VOLUME IN DM^3) OF *C. RODERICKII* PLANTS FOUND ON THE BURNED PLOTS IN JUNE 1989. Inds. = individuals.

Size class (dm^3)	n	Fruiting (% of inds.)	Production of rooted branches (% of inds.)
0–10	67	19	10
10–20	7	57	29
20–30	13	38	46
30–40	7	100	86
> 40	3	100	33

duced at least one rooted branch (15 plants with one rooted branch, and 7 with more than one rooted branch). Not surprisingly, production of rooted branches varied significantly with plant size (contingency table analysis; $\chi^2 = 26$, df = 4, $P < 0.0001$) and was concentrated in the larger size classes of plants (Table 2). Inspection of Table 2 shows that the smallest size class had relatively few plants producing rooted branches (10%), whereas many plants (≥29%) in the 20–30 and 30–40 dm^3 size classes were producing rooted branches by 1989. Altogether, rooting of branches contributed close to a third (27%) of the rooting points counted outside of the herbivore exclosures in the burned plots in June 1989. In addition, a number of larger plants had at least one arching branch touching the soil, and likely soon formed rooting points.

Comparison of rooting points in each plot postfire against the number counted prefire provides a measure of the degree of recovery of the burned plot populations. By June 1989, only one burned plot contained more rooting points than it had contained prefire. Most of the other plots had very few rooting points: three plots had just 1 or 2. The 1989 density of rooting points per plot was 3.8 ± 1.5 (SE). This was 25% of the prefire mean value of 15.5 (Table 1) and was significantly less than the prefire rooting point density (paired t-test: t = 4.8, df = 8, P = 0.0014). However, the contribution of branch layering to rooting point density was important for some plots. When April 1986 counts of surviving plants were compared to June 1989 counts of rooting points, four of the nine plots showed increases in rooting point counts in 1989. Because germination and seedling establishment had ceased on burned plots by 1986, this increase in rooting points indicated that branch layering had begun to reverse decreases in plant density that occurred during the first several postfire seasons because of mortality of individual plants (e.g., Fig. 1).

Herbivore Exclosures

Seedlings protected by exclosures had higher survival rates than those in open plots (Fig. 3). Most plants in either treatment category died during the late spring and summer of the first year (days 46–211, Fig. 3). Many of these dead plants were noted standing dried but intact and probably were killed by drought. During visits after 20 August 1984 (day 150), I noted damage by vertebrate herbivores (clipping of stems) to plants in open plots and one case of the burial of a plant by activities of a pocket gopher. The loss of these plants contributed to the decline in survival of open plants during that time (days 150–250), whereas most exclosed plants survived during that period (Fig. 3). By the second spring

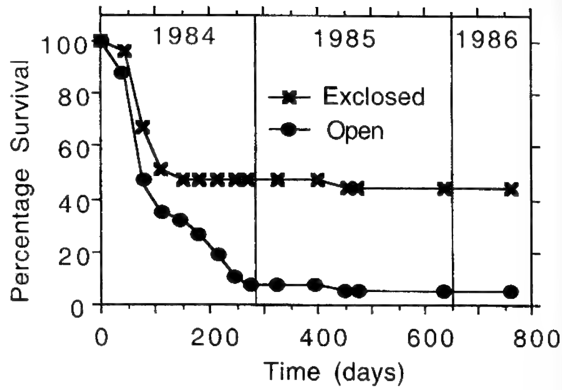

FIG. 3. Survival of seedlings in exclosed or open subplots of burned plots from 23 March 1984 until 25 April 1986. Time in days is measured from 23 March 1984, when 45 seedlings were counted in exclosed plots and 37 in open plots.

after the plots were burned (20 May 1985, day 423), 44% of exclosed plants had survived in contrast to just 5% of open plot plants. Survival analysis showed the two groups of plants differed significantly in their survival patterns (Peto-Peto-Wilcoxon rank test, P = 0.0016).

Discussion

Fire killed mature plants of *C. roderickii* and stimulated seed germination. The failure of burned mature plants to resprout is consistent with reports for other species in the subgenus *Cerastes* (e.g., Keeley and Zedler 1978; Keeley and Keeley 1988).

Stimulation of seed germination by heat from fire is also unsurprising: Keeley (1991) listed 24 species of *Ceanothus* for which germination is stimulated by heat. My results also suggest that seeds of *C. roderickii* require stratification for germination, which has been shown for some species of *Ceanothus*, and previously reported for *C. roderickii*. Studies of certain other *Ceanothus* species, e.g. Quick (1935) and Bullock (1982), have shown that heat treatment followed by cold (< 2.5°C) gives greatest germination. Also, James (1996) reported that *C. roderickii* germinated best when treated by heat followed by cold conditions. In my laboratory study, seeds germinated only after heat treatment was followed by stratification. Although did not contain a stratification-no heating treatment, seedlings were found in the field in late winter and spring, which also is consistent with a stratification requirement for *C. roderickii* germination.

Some germination occurred in control plots each year, however, showing that germination is not completely dependent on fire. Limited germination of other *Ceanothus* species in unburned chaparral stands has been reported

(Keeley 1992), either because soil surface temperatures on open sites in summer are sufficient to stimulate germination of some seeds (Keeley and Keeley 1981) or because a small percentage of seeds are nonrefractory (Keeley 1987). However, establishment of *Ceanothus* is generally limited to postfire conditions as seedlings germinating in unburned chaparral usually die (Keeley 1992). That was the case in this study (Fig. 1).

Despite the germination of seedlings each season in plots that were not burned, recruitment was almost completely limited to seedlings in plots that had been burned during the first postfire season (Fig. 1). Thus, changes in site conditions that follow fire (e.g., increased soil nutrients, decreased competition from other plants) likely aid successful seedling establishment. This is consistent with other *Ceanothus* species discussed by Keeley (1991), in which recruitment generally occurs from seeds that germinate in the first season postfire, despite some seeds geminating in second or later postfire seasons.

Mortality of *C. roderickii* seedlings on burned plots was greatest in the first season postfire (Fig. 1). This result is similar to that of many other chaparral studies of postfire seedling demography (Keeley and Keeley 1988). For example, Kummerow et al. (1985) documented 92% mortality of *C. greggii* seedlings during the first postfire growing season. That study, as well as others such as Thomas and Davis (1989), Moreno and Oechel (1992), and Tyler and D'Antonio (1995), provide further evidence that water availability limits postfire *Ceanothus* seedling survival. The shriveled yet undamaged appearance of most dead *C. roderickii* seedings in my study also implied drought as a major mortality factor. It has been suggested that seedlings of seeder plant species are more drought-tolerant than those of sprouters (Parker 1984), but a recent study by Schwilk and Ackerly (2005) found no evidence of differential drought tolerance of obligate seeder compared to sprouter *Ceanothus* species.

Herbivory was a secondary cause of *C. roderickii* mortality. Although some herbivore damage was observed during the summer of 1984, most herbivore damage (apparently browsing by mammals) was observed in the second postfire season (1985). By the end of the second season, seedlings in exclosed subplots were significantly longer-lived than those in open plots (Fig. 3). Although there was no control (open sided) exclosure treatment that allowed me to explicitly separate the shading effect of an exclosure from its protective effect against herbivory (e.g., Martens and Boyd 2002), observations of browse damage to plants in open subplots support the interpretation that herbivore damage in those subplots was a major contributor to plant mortality. This result is similar to that of Mills (1986), except that he found significant insect herbivory in addition to significant effects of mammalian herbivores. Insect herbivory also was reported as a significant factor in postfire survival of *C. greggii* (Moreno and Oechel 1992). In my study, I noticed insect damage to fruits of *C. roderickii* but not major damage to foliage.

As with many plants (Klinkhamer et al. 1997), including some species of *Ceanothus* (e.g., Zammit and Zedler 1993), fruit production was greater by larger *C. roderickii* plants. Branch layering also was more likely to occur for larger *C. roderickii* plants. This fact emphasizes the importance of larger *C. roderickii* individuals to population recovery as they are able to both contribute more seeds to the seed bank and increase rooting point density through branch layering.

Keeley (1992) pointed out that seeder species generally have single aged cohorts of stems, whereas resprouters may have multiple age stems on individual shrubs. Although my data confirm *C. roderickii* as a seeder species, its branch layering ability allows it to add stems (via branch layering) to its population long after postfire seedling establishment ends. For *C. roderickii*, branch layering was first documented in the sixth season postfire. It probably accelerated in subsequent seasons, as smaller plants grew branches long enough to root and as branches with one rooting point added additional rooting points. One consequence was that, unlike other seeder species, the density of *C. roderickii* (as measured by rooting points per unit area) began to increase in some plots once branch layering began. Thus, postfire recovery of *C. roderickii* populations covers a much longer timeframe than for *Ceanothus* species that do not branch layer. In contrast to other *Ceanothus* species studied to date, population density of *C. roderickii* is not determined solely by germination followed by postfire seedling mortality. For example, one of the burned plots had 74 rooting points prefire and produced 36 seedlings in 1984, but by 1986 only 4 plants remained. However, in June 1989 branch layering had resulted in a count of 8 rooting points on that plot, doubling the plot's rooting point density. It is interesting to note that *Arctostaphylos*, another dominant California chaparral genus that contains both seeder and sprouter species (Keeley and Keeley 1988), contains several low-growing (prostrate to spreading) taxa that are reported to root at the nodes (Hickman 1993): *A. hookeri* G. Don subsp. *hearstiorum* (Hoover and Roof) P. Wells; *A. parryana* Lemmon; and *A. patula* E. Greene. Some populations of *A. patula* are reported to resprout following fire (Wells 1968) and thus may have a mix of traits (sprouting and branch

layering) that could represent a unique postfire recovery strategy.

The results of this study have application to rare species management. When this study was conducted, the response of *C. roderickii* to fire was unknown and hence managers of the Pine Hill Ecological Reserve were reticent to conduct a prescribed burn. Because this study showed that *C. roderickii* germination is stimulated by fire and therefore populations can recover, that burn took place. This leads to the question of how often such burns should be conducted to maintain the chaparral on the Pine Hill Reserve. As a seeder species, *C. roderickii* depends on recruitment from the seed bank in order to re-establish populations after fire. Keeley and Keeley (1988) state that obligate seeding species require 5–15 yr to produce substantial seed crops. This is probably the case with *C. roderickii*, for which notable flowering and fruit production occurred in the sixth season postfire (1989, when about one-third of plants flowered). Although replenishment of the seed bank probably began at that point, it is unknown how long it takes to return the *C. roderickii* seed bank to adequate levels for postfire stand regeneration. Seed predation by mammals and birds probably destroys considerable numbers of the seeds produced by chaparral shrubs (Keeley 1977; Davey 1982; Kelly and Parker 1990; Boyd and Serafini 1992; O'Neil and Parker 2005). Furthermore, studies of other chaparral species imply that fires themselves cause considerable mortality of seeds in soil (Keeley 1977; Odion 2000; Odion and Davis 2000; Odion and Tyler 2002). Thus, it seems prudent to allow *C. roderickii* populations sufficient time to adequately build up the seed bank before another prescribed fire is conducted on the Pine Hill Ecological Reserve.

Odion and Tyler (2002) also proposed a long postfire recovery period for the federally endangered *Arctostaphylos morroensis*, an obligate seeder species that may need more than four decades to build up a seed bank adequate to replace the prefire population. However, a crucial difference between *C. roderickii* and *A. morroensis* is the branch layering ability of *C. roderickii*. Odion and Tyler (2002) found that high postfire seedling mortality of *A. morroensis* reduced recovering population density to less than that of the original stand. As a result, the new *A. morroensis* population was significantly smaller (< 50% by 3 yr postfire) than the original: the prescribed burn resulted in a net loss of individuals of this endangered species. In my study, by 1986 seedling mortality had reduced plant density (rooting points) to below prefire levels in all but one plot (overall *C. roderickii* density was 25% of that prefire). However, the branch layering ability of *C. roderickii* allowed density to increase between 1986 and 1989 in four plots. Plant numbers on all plots rose from 136 (in 1986) to 138 (in 1989) despite mortality of 29% of plants between 1986 and 1989. By 1989, branch layering had produced 27% of the rooting points counted and branch layering was just beginning at that time. Continuation of branch layering should enable *C. roderickii* to continue recovery toward prefire densities in most if not all plots. This illustrates the importance of branch layering to postfire recovery of this federally endangered obligate seeding chaparral species.

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THE EFFECT OF STAMINODE REMOVAL ON FEMALE REPRODUCTIVE SUCCESS IN A WYOMING POPULATION OF THE ENDANGERED BLOWOUT PENSTEMON, *PENSTEMON HAYDENII* (SCROPHULARIACEAE)

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ABSTRACT

We examined the effect of removing the staminode of the rare Blowout penstemon, *Penstemon haydenii*, on female reproductive success in a south-central Wyoming population. We found no significant difference in fruit set or in seeds per fruit between flowers with and without staminodes. The most frequent flower visitor, the megachilid bee, *Osmia brevis*, modified its behavior when visiting flowers without staminodes. In intact flowers, *O. brevis* collected pollen by straddling the staminode and rubbing its head and thorax across the anthers. In flowers without staminodes, *O. brevis*, appeared to compensate for the increased distance to the anthers from the corolla floor by simply stretching its legs to make contact with the anthers. The smaller, native generalist sweat bee (*Dialictus pruinosus*), which commonly collected pollen in intact flowers, appeared disoriented in flowers without staminodes, and frequently left without collecting pollen. Other taxa (e.g., bumblebees, *Bombus* spp., the masarid wasp *Pseudomasaris vespoides*), appeared unaffected and plied the flowers without incident. We speculate that the staminode of Blowout penstemon is intermittently vestigial: where *O. brevis*, bumblebees, and *P. vespoides* are common, the staminode is of little consequence; where *D. pruinosus* is the primary pollinator, the staminode is essential to sexual reproduction by the plant.

Key Words: bees, behavior, fecundity, *Penstemon*, pollinators, staminode.

Staminodes are stamens that have lost their essential male reproductive function: they no longer produce viable pollen and, in most instances, are antherless. Although not common, staminodes are found in about one-third of all Angiosperm families (Walker-Larsen and Harder 2000). They have evolved diverse shapes and functions (Ronse Decraene and Smets 2001), all seemingly related indirectly to sexual reproduction. For example, they may function as nectar guides (Delpino, cited in Straw 1956), act as a barrier to discourage flower entrance by nectar or pollen thieves (Straw 1956), provide a purchase to flower visitors (Pennell 1948), act as a lever mechanism to enhance pollination (Torchio 1974; Walker-Larsen and Harder 2001), or provide fodder to potential insect pollinators (Cane 1993). Or, they currently may serve no discernible function (Walker-Larsen and Harder 2001).

Staminodes are particularly common in the tribe Cheloneae (Scrophulariaceae), where they are thought to have accompanied the evolution of zygomorphic flowers (i.e., Endress 1999; Ronse Decraene and Smets 2001). In the genus *Penstemon*, staminodes are one of the defining characteristics: two pairs of fertile stamens, an upper and a lower, are positioned along the abaxial surface of the corolla, and the fifth sterile stamen, the staminode, curves down to lie along the adaxial corolla "floor". The staminode is often densely pubescent, hence the common name, "beardtongue," for the genus. The staminode may be exerted, as in *P. eriantherus*, or extremely short and perpendicular to the corolla roof (e.g., *P. personatus*). These differences may be associated with the kind of primary pollinator that visits the flowers. Many of the hypotheses cited above to explain the evolution of staminodes have been presented with *Penstemon* in mind, but only recently have experimental studies begun to uncover the role of these structures (Walker-Larsen and Harder 2001; Dieringer and Cabrera R. 2002).

In this paper, we evaluate whether the staminode of Blowout penstemon, *Penstemon haydenii* S. Wats., plays a role in increasing female reproductive success of this rare species, and if the results differ with species of flower visitor (e.g., Dieringer and Cabrera R. 2002).

Penstemon haydenii is an early successional perennial herb of "blowouts" in sparsely vegetated, active sand dunes in western Nebraska and south-central Wyoming (Hardy et al. 1989; Stubbendieck et al. 1989; Heidel 2005). It has large (c. 25–30 mm), fragrant pale blue to lavender or pink flowers arranged in whorls (verticillasters) along the inflorescence. The staminode is included in the corolla, and is flattened

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at the distal end where it is densely to sparsely pubescent (or even glabrous) with yellow to golden hairs. Flowers are cross-pollinated and self-incompatible (Tepedino et al. 2006a, b). Nebraska and Wyoming populations are visited by a range of insects (Lawson et. al. 1989; Tepedino et al. 2006a, b; unpublished) but are pollinated primarily by native bees in the families Megachilidae, Halictidae and Apidae (Tepedino et al. 2006a, b). It has been listed as Endangered under the U. S. Endangered Species Act since 1987.

Methods

We studied *P. haydenii* in the sand dunes of northwest Carbon Co., south-central Wyoming, USA, in June 2005. The Bear Mountain East site is situated on the south slope of Bear Mountain in a blowout depression in the Ferris Dunes (Stokes and Gaylord 1993) at the eastern end of the Ferris Mountains (2035–2270 m elevation). The *P. haydenii* ramets (c. 2000; Heidel 2005) grow among lemon scurf pea (*Psoralea lanceolata* Pursh.), chokecherry (*Prunus virginiana* L.), silverleaf phacelia (*Phacelia hastate* Dougl. Ex Lehm.), and painted milkvetch (*Astragalus ceramicus* Sheld. var. *filifolius* (A. Gray) Herm.). Average precipitation in the area is about 25 cm yr^{-1}, most falling in April and May. Consult Heidel (2005) for detailed site descriptions with maps and pictures.

Observations of flower phenology were made twice, once at the beginning of the blooming season (c. June 8) and again, about two weeks later when bloom was waning. Each time, ten fresh flowers (one on each of ten haphazardly selected plants) were observed for several successive days, from the beginning of anthesis to senescence. Anther dehiscence, stigma receptivity, and style position were noted.

To test for the role of the staminode in female reproductive success, we haphazardly selected 25 mature plants scattered throughout the population with an inflorescence with several mature, but unopened, buds in each of several flower whorls, and no open flowers. Inflorescences were bagged with white nylon tulle (1-mm^2 mesh) to prevent insect visitation before staminodes had been excised. To resist the frequent strong winds, the bag was anchored to the ground with metal wire. An additional unbagged inflorescence of similar age was chosen from a nearby plant as a control. As the buds opened on the bagged inflorescence, the staminode in two (rarely one) open flowers per node (up to eight flowers per inflorescence) was excised at the base with fine scissors while being held with forceps. Care was taken not to brush against the stamens and stigma during excision. For comparison, at least three flowers on each control treatment inflorescence were selected and marked with a paint pen. Fruits were collected in July 2005, air-dried in the lab and seeds were counted.

We compared fruits per flower and seeds per fruit between treatments using non-parametric statistical tests. Because not all whorls on each selected plant matured flowers, the distribution of treated flowers varied both across whorls and plants. We used the Chi square statistic to 1) compare fruit set among flowers of different whorls whose staminode had been removed, and 2) between the staminode removal treatment and controls. The Kruskal-Wallis test was used to compare seeds per fruit among different flower whorls whose staminode had been removed. Seeds per fruit between removal treatment and controls were compared using the Wilcoxon Rank Sum Test (also known as the Mann-Whitney test).

Behavior of abundant insect foragers on flowers with and without staminodes was observed and recorded soon after treatment during four 30-minute periods over two days.

Results

The developmental tempo of flower maturation accelerated with time. At the beginning of the blooming season, flowers remained open for four to seven days. The outer pair of anthers typically dehisced on the second day and the inner pair the next day. The downward hook in the style, normally taken to signify stigma receptivity (Straw 1956; but see Tepedino et al. 1999) occurred by the second day (i.e., at the same time the outer pair of anthers were dehiscing). Flowers of later-blooming plants had flowers that opened and senesced in one to two days. Both pairs of anthers dehisced and the style hooked on the first day. Both maturation sequences are unusual in *Penstemon* because the style usually does not bend below the anthers until after the anthers dehisce (see also Tepedino et al. 1999).

Plants in the treatment groups, particularly the open-pollinated treatment, were heavily browsed by cattle and wild ungulates. Nine of the inflorescences used for staminode removals and almost all of the control inflorescences on adjacent plants were cropped, forcing us to compare open-pollinated control plants from a concurrent breeding system study (Tepedino et al. 2006b) with the treatment flowers.

Before comparing results from the staminode removal experiments with controls, we compared fruits per flower and seeds per fruit among the four flower whorls (Table 1). There was no difference among whorls in fruits per flower ($\chi^2 = 7.44$, df = 3, $P > 0.05$) or in seeds per fruit (Kruskal-Wallis Test, df = 3, $P > 0.40$) for the staminode removal treatment; we therefore com-

TABLE 1. THE NUMBER OF FLOWERS PRODUCING FRUITS (FRTS) OR NO FRUITS (NOFRTS) FOR STAMINODE REMOVAL AND OPEN-POLLINATED TREATMENTS IN A WYOMING POPULATION OF *PENSTEMON HAYDENII*. N = number of plants with treated flowers in each category. Staminode removed treatment combines data from Whorls 1–4. Seeds/Frt data are plant means and standard deviations.

	Frts	NoFrts	N	Seeds/Frt	SD
Staminode Removed	60	26	16	12.5	2.9
Open Pollinated	21	7	10	15.9	6.2
Whorl 1	24	3	14	11.0	5.3
Whorl 2	14	11	13	12.0	6.5
Whorl 3	14	7	11	14.5	5.5
Whorl 4	8	5	7	12.9	3.0

bined the data for comparison with the open-pollinated treatment.

We found no difference in fruit set between the staminode removal flowers and the open-pollinated treatment (Table 1; $\chi^2 = 0.28$, df = 1, $P > 0.50$). Nor was there a difference in seeds per fruit between treatments (Wilcoxon Rank Sum Test, $P > 0.30$). Apparently, female reproductive success was little influenced by the absence of the staminode.

The most abundant visitors to the flowers of Blowout penstemon were bees of the genera *Osmia* (especially *O. brevis*), *Dialictus* spp., *Bombus* spp. and the masarid wasp, *Pseudomasaris vespoides,* a specialized *Penstemon* visitor (Cooper 1952). All were seen visiting flowers with and without staminodes. In some cases, the floral visitors modified their behavior on the flowers without staminodes. For example, on intact flowers, *O. brevis* females would land on the staminode and rub their head and thorax back and forth on the anthers to collect pollen, concurrently contacting any stigma that had reached the hooked stage). When visiting flowers without a staminode, *O. brevis* landed on the floor of the corolla and stretched upwards to reach the anthers. We saw no indication, either in observations, or when modest pressure was applied to the staminode, of declination of the stamens or style as occurs when the staminode functions as a lever (Torchio 1974).

Dialictus females seemed disoriented by staminode removal. In staminodeless flowers, they appeared unable to gain a purchase on the corolla floor and soon left. Normally, they spent much time on the flowers, crawling around inside the corolla, perhaps to collect nectar; frequently resting on the staminode or walking over the stamens and anthers in an inverted position to become dusted with pollen on the ventral abdomen. In general, *Dialictus* females spent more time on the flowers than did other bees. (Dieringer and Cabrera R. 2002 also found that small bees spent longer times on the flowers than did large bees.)

Two visitors did not modify their behavior. *Pseudomasaris vespoides* females exhibited the same pollen collecting technique in flowers with and without staminodes. Like *O. brevis*, they collected pollen by scraping their heads against the anthers. However, because of their size, female *P. vespoides* had no difficulty in reaching the anthers. Similarly, *Bombus* spp. did not show any obvious behavioral changes when visiting flowers with staminodes removed.

DISCUSSION

The production of an elaborate staminode, as in Blowout penstemon, would seem to entail a non-trivial cost of energy and nutrients. One expects such an expenditure to be compensated for by a benefit, such as an increase in reproductive success. Recently, two groups have followed early studies by Clements and Long (1923) by removing the staminodes of five species and examining the effects on female and male reproductive success (Dieringer and Cabrera R. 2001, 2002; Walker-Larsen and Harder 2001). Their results suggest that the function of the staminode in *Penstemon* species is diverse, and that even well-developed, costly staminodes may not have an obvious function. Results of staminode removals by Clements and Long (1923) were also species-specific; our findings support that interpretation.

Walker-Larsen and Harder (2001) examined four species, two bird-pollinated (*P. centranthifolius*, *P. rostriflorus*) and two bee-pollinated (*P. ellipticus*, *P. palmeri*), with very different results. The bird-pollinated species exhibited no effect of staminode removal, either on pollen deposition on the stigma, or pollen removal from the anthers. Results for the bee-pollinated species were more complicated: pollen deposition on the stigma decreased significantly for flowers without staminodes but the mechanism of action was different for *P. ellipticus* and *P. palmeri*. Pollen removal was significantly greater from anthers in intact *P. palmeri* flowers than from flowers without staminodes. However, greater pollen removal rates need not translate to greater male fitness: that depends on whether pollen is deposited on a receptive stigma or is removed from the system either by grooming or by being using as larval food (Thomson and Thomson 1992; Kobayashi et al. 1999). In *P. ellipticus*, pollen removal was unaffected by staminode removal.

The work of Dieringer and Cabrera R. (2001, 2002) also shows an effect of staminode removal on female reproductive success of a bee-pollinated species, *P. digitalis*. Initially (2001), they showed that flowers with staminodes removed

produced significantly fewer seeds per fruit than intact flowers. Subsequently, they showed that staminode removal affected pollen deposition on the stigma but not pollen removal from the anthers (Dieringer and Cabrera R. 2002) and that the size of flower-visiting bees was important: both large and small (but not intermediate-sized) bees deposited fewer pollen grains in staminode-less flowers. Thus, for all three bee-pollinated species studied thus far, pollen deposition per visit is reduced by staminode removal. In contrast, male reproductive success may have been lower in only one of the three species.

Time constraints prevented us from estimating pollen deposition and removal. Instead, we used a simple bioassay to compare fruit set and seed production between flowers with staminodes and flowers whose staminodes were removed (Dieringer and Cabrera R. 2001). In contrast to Walker-Larsen and Harder (2001) and Dieringer and Cabrera R. (2001, 2002), we found no effect of staminode removal on female reproductive success of this bee- and wasp-pollinated beard-tongue.

Our result would appear to be another example of species-specific differences. Evidently, it is not simply that the staminode is superfluous in bird-pollinated species and functional in bee-pollinated species as found by Walker-Larsen and Harder (2001). *Penstemon haydenii* may be a bee-pollinated species whose staminode function is dependent upon the pollinators that service it. The behavior of larger bees and wasps (*Osmia*, *Bombus, Pseudomasaris*) on flowers without staminodes seemed unlikely to depress either pollen delivery or removal. Conversely, the much smaller *Dialictus* bees completely changed their behavior on flowers without staminodes such that pollination was unlikely. Similarly, Dieringer and Cabrera R. (2002) showed that pollen delivery was pollinator-size dependent; intermediate sized bees (but not small or large bees) were unaffected in pollen delivery by absence of a staminode. These results are not novel: Clements and Long (1923) long ago reported that some foraging bees are unperturbed by many types of experimental flower modifications.

We suspect that the staminode of Blowout penstemon may influence reproductive success only in some years and at some sites, when smaller visitors like *Dialictus pruinosus* predominate. Whether this occurs frequently enough to support the continued presence of the staminode in this species over the long term is an open question.

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INTRASPECIFIC VARIATION IN SEED IMBIBITION OF BLACKBRUSH (*COLEOGYNE RAMOSISSIMA*: ROSACEAE).

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ABSTRACT

Intraspecific variation in blackbrush (*Coleogyne ramosissima* Torr.) seed imbibition was quantitatively investigated in the Mojave Desert. Blackbrush seeds were collected from six isolated mountain ranges, with each range sampled from one high-elevation (1550 m) and one low-elevation (1200 m) location for a total of 12 populations. Under laboratory experimental conditions, seed dry mass and initial seed moisture content did not differ significantly among the 12 populations. High-elevation source seeds imbibed significantly more water than low-elevation source seeds, and this was likely associated with habitat-specific selection. However, differences in full imbibition among seed collection sites at the identical elevation were not significant. Germination of field-collected seeds was similar, ranging from 87 to 93% among the 12 populations. Results of this study suggest that among six isolated mountain ranges in the Mojave Desert, blackbrush seed imbibition varies with elevation, but not with latitude.

Key Words: blackbrush, *Coleogyne ramosissima*, interspecific variation, Mojave Desert, seed imbibation.

Blackbrush (*Coleogyne ramosissima* Torr., Rosaceae) is often a dominant shrub species on shallow soils in the transition zone between North American warm Mojave Desert and cold Great Basin Desert (Bowns 1973; Bowns and West 1976; Meyer and Pendleton 2005). *Coleogyne ramosissima* is a mast-seeding species, producing abundant seed crops at intervals of a few to several years, with vegetative growth occurring at more frequent intervals (Pendleton and Meyer 2004). This species exhibits variation in seed dormancy (Lei 1997; Pendleton and Meyer 2004; Meyer and Pendleton 2005). Seeds collected from low-elevation sites are less dormant than seeds collected from high-elevation sites in southern Utah and Nevada (Lei 1997; Pendleton and Meyer 2004). *Coleogyne ramosissima* may also exhibit variation in the relative ability to imbibe water during germination. Such variation is often interpreted as a result of habitat-specific selection (Pendleton and Meyer 2004).

The objective of this study was to evaluate intraspecific differences in imbibition characteristics under controlled laboratory conditions for blackbrush seeds from various elevations and latitudes. I hypothesized that *C. ramosissima* seeds from different environmental conditions within the Mojave Desert would exhibit intraspecific variation in their relative ability to imbibe water.

From late June through early August 2005, *Coleogyne ramosissima* seeds were collected from six isolated mountain ranges in the Mojave Desert, with each range sampled from one high-elevation (1550 m) and one low-elevation (1200 m) location for a total of 12 populations (Table 1). The Spring Mountains, Newberry Mountains, and McCullough Range are located in southern Nevada; the Clark Mountain is located in southeastern California; the Mormon Range in southwestern Utah; and the Virgin Mountains in northwestern Arizona. An unusually large amount of rainfall occurred in late winter and early spring, and abundant seed crops were produced (Lei, personal observation). For this reason, no attempts were made to examine variation in full imbibition at the same or similar seed age.

A total of 2400 filled seeds were randomly collected from *C. ramosissima* shrubs and adjacent soil surfaces among the 12 populations. Because some seeds were collected from the soil surface the exact age of all seeds was difficult to determine.

All flattened, punctured, and wrinkled (damaged) seeds were discarded in the field. In the laboratory, full-sized but empty, inviable seeds were removed by floating off the unfilled fruits in water. Floating seeds were further examined for viability using a cut test, and empty seeds were discarded. To obtain maximum germination, filled seeds were stored at 4°C for six weeks in the dark (dry-chilling) prior to an imbibition experiment (Meyer and Pendleton 1990; Lei 1997).

Within each of the 12 populations, a total of 100 seeds were randomly selected, and placed in an oven, dried at 40°C for 36 hr to determine seed dry mass and initial moisture content. Seeds were weighed to the nearest 0.001 g with a digital

TABLE 1. SEED DRY MASS, INITIAL SEED MOISTURE CONTENT, IMBIBITION, AND OVERALL GERMINATION PERCENTAGE OF FILLED SEEDS FROM SIX ISOLATED MOUNTAIN RANGES IN THE MOJAVE DESERT. High-elevation sites were located at 1,550 m, and low-elevation sites were at 1200 m (n = 100 per elevation in each mountain range). Mean values other than germination percentages are expressed with standard errors.

Mountain range	Coordinates (*Lat.Long.*)	Elevation (*m*)	Seed mass (*mg*)	Moisture content (*%*)	Imbibition (*% wt. gain*)	Germination (*%*)
Clark Mountains, CA	35°21′N, 115°33′W	1200	22.7 ± 0.5	4.4 ± 0.1	17.8 ± 2.5	87
	35°41′N, 115°35′W	1550	21.6 ± 0.6	5.1 ± 0.2	22.4 ± 1.9	92
McCullough Range, NV	35°49′N, 115°11′W	1200	22.2 ± 0.5	4.9 ± 0.2	18.5 ± 2.3	88
	35°48′N, 115°09′W	1550	21.7 ± 0.4	5.6 ± 0.3	22.9 ± 1.7	90
Mormon Range, UT	37°05′N, 113°57′W	1200	21.4 ± 0.6	4.9 ± 0.2	18.6 ± 1.8	92
	37°04′N, 113°56′W	1550	21.5 ± 0.5	5.1 ± 0.2	21.9 ± 2.1	93
Newberry Mountains, NV	35°16′N, 114°42′W	1200	21.2 ± 0.6	4.8 ± 0.2	18.5 ± 1.5	92
	35°16′N, 114°43′W	1550	19.6 ± 0.4	5.3 ± 0.2	25.0 ± 2.0	93
Spring Mountains, NV	36°09′N, 115°44′W	1200	21.7 ± 0.6	5.0 ± 0.3	18.7 ± 1.9	90
	36°10′N, 115°42′W	1550	21.0 ± 0.5	5.1 ± 0.3	23.6 ± 2.7	88
Virgin Mountains, AZ	36°37′N, 114°09′W	1200	23.1 ± 0.6	4.9 ± 0.3	17.5 ± 2.7	91
	36°38′N, 114°08′W	1550	22.7 ± 0.6	5.0 ± 0.3	23.9 ± 2.1	89

balance scale (Ohaus Voyager PRO Precision Balance). Seed moisture content was computed using the following equation: (Fresh weight - dry weight/fresh weight) * 100 (Bewley and Black 1994). Seeds used for measuring initial moisture content were not used again for the imbibition experiment due to possible damage to embryos and/or endosperm tissues.

During the imbibition experiment, seven replications of 14–15 seeds were included in each population. Seeds were placed in 100-mm plastic Petri dishes between two moistened germination blotters. Seeds were incubated at 4° C in the dark for approximately 5 wk without light to decrease evaporative water loss, but were briefly exposed to soft-white fluorescent lights as seeds were pat-dried and weighed daily. Seeds were pat-dried with paper towels to remove free water on their seed coat before weighing. All 12 seed populations received 5 mL of water biweekly. Imbibition, the absorption of water by nonliving or senescent materials and subsequent swelling caused by adhesion of the water to internal surfaces of materials, is the initial step in seed germination (Bradford 1995; Jorgensen and Chesser 2000). At the end of the incubation period, all ungerminated seeds were examined for viability using a cut test. Germination percentage values were corrected for seed viability (Meyer and Pendleton 2005).

Germination percentage of filled seeds in each of the 12 populations was computed. Two-way Analysis of Variance (Analytical Software 1994) was performed on seed dry mass, initial seed moisture content, and mass at full imbibition (i.e., percent gain in mass), with elevation and latitude as main effects. Pearson's correlation (Analytical Software 1994) was conducted to correlate seed germination percentage with water content at full imbibition. Mean values and standard errors were calculated, and statistical significance was determined at $P \leq 0.05$.

Across the Mojave Desert, it is common for *C. ramosissima* seeds to reach full size but fail to fill. Unfilled and/or damaged seeds ranged from 32% in the Virgin Mountains to 44% in the Spring Mountains, with both extreme percentages occurring at the low-elevation sites.

Nevertheless, seed dry mass and initial seed moisture content did not differ significantly among six latitudes or between high and low elevation (ANOVA, $F_{11,1188} < 1.02$, $P > 0.05$; Table 1). The elevation * latitude interaction was also not statistically significant for seed dry mass (ANOVA, $F_{11,1188} = 1.00$, $P > 0.05$) and initial seed moisture content (ANOVA, $F_{11,1188} = 0.44$, $P = 0.5551$; Table 1), indicating that these two traits were similar among the 12 seed populations.

Seeds gain some mass immediately upon wetting among filled seeds. Seeds imbibed water at a similar rate regardless of collection site. The greatest imbibition occurred during the first four days, and then increased slowly with slight oscillations. Seeds generally reached a maximum imbibition weight after 12 d. Differences in water content at full imbibition did not affect the timing of germination. No consistent pattern was found between differences in imbibition and the timing of germination. Germination of most seeds was observed within 2–3 wk of the initial experiment, and germination occurred within a few days after full imbibition regardless of collection site.

Coleogyne ramosissima seeds collected from high-elevation sites imbibed significantly more water (ANOVA, $F_{11,1188} = 56.17$, $P \leq 0.0001$; Table 1) compared to seeds collected from low-elevation sites. However, differences in water content at full imbibition among latitudes at the same elevation were not statistically significant (ANOVA, $F_{11,1188} = 0.59$, $P = 0.7071$; Table 1).

Similarly, the elevation * latitude interaction was not statistically significant (ANOVA, $F_{11,1188}$ = 1.02, P = 0.4531; Table 1), indicating that water content at full imbibition was similar in all 12 seed populations at similar elevations.

The overall germination percentages were similar among the 12 populations, ranging from 87% at the low-elevation site in the Clark Mountain to 93% at the high-elevation site in the Mormon Range. Correlation between germination percentage of filled seeds and water content at full imbibition was positive and highly significant (df = 10, r = 0.88, P $\leq$ 0.001).

The direction of selection on *C. ramosissima* seed imbibition trait may depend on local environmental conditions. My data indicate that imbibition of seeds varies as a function of elevation among populations. This variation suggests selection for seed imbibition in response to climate and differences in maternal environmental conditions.

However, no latitudinal variation in imbibition was found in this study. The lack of significant variation at the identical elevation in spatially separated mountain ranges may not reflect past selection for latitudinal differences within the relative small (geographically restricted) Mojave Desert.

Results of this study indicate the existence of habitat-correlated variation in seed imbibition response for *C. ramosissima*. Intraspecific variation in seed imbibition was found, a threshold trait, between two distinct elevations under controlled laboratory conditions. Seeds collected from low-elevation sites imbibed significantly less water, whereas seeds collected from high-elevation sites imbibed more water during the imbibition experiment. Since maternal plants were growing under different environmental conditions, these differences may be due to habitat-specific selection. Variation in *C. ramosissima* seed imbibition was probably a result of evolutionary fine-tuning in response to variation in local environmental regimes. In these mountain ranges, moisture availability changes with elevation and may have selected for the observed differences in seed imbibition between higher and lower elevations.

Although the ecological consequences of differences in imbibition in general or for other plant species remain poorly understood, *C. ramosissima* seeds collected from low-elevation sites have responded to soil moisture limitation by imbibing less water than seeds collected from high-elevation sites. Due to a predictable hot and dry environment at low elevations, selection should favor seeds that imbibe less water prior to germination compared to high elevations in the Mojave Desert.

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SUPERNUMERARY CHROMOSOMES IN *ERIOPHYLLUM LANATUM* AND *E. CONFERTIFLORUM* VAR. *CONFERTIFLORUM* (ASTERACEAE)

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ABSTRACT

Chromosomes in excess of the basic complement have been known for 100 years. Nevertheless, in most species the role of supernumerary or B chromosomes remains unknown or speculative. Here, I describe the frequency, distribution, and transmission to progeny of supernumerary chromosomes in two widely distributed western North American polyploid complexes. Meiotic analyses of microsporocytes found one to four supernumerary chromosomes in 14% of the 293 populations examined in *Eriophyllum lanatum*, and one, two, or six supernumeraries in 15% of the 133 populations examined in *E. confertiflorum* var. *confertiflorum*. Most supernumerary chromosomes were in the size range of A chromosomes, indistinguishable from As, and did not pair with them. Artificial hybridizations showed that the supernumerary chromosomes were transmitted by either parent. Populations with supernumerary chromosomes were nonrandomly distributed in both species. Intervarietal or interspecific hybridization may be responsible for some of their nonrandom distribution in *E. lanatum*. Supernumerary chromosomes may be involved in the dysploid chromosome numbers in *Eriophyllum*.

Key Words: Asteraceae, dysploidy, *Eriophyllum*, polyploid complex, supernumerary chromosome distribution, supernumerary chromosome frequency, and supernumerary chromosome transmission.

Wilson (1925, pp. 872–878) referred to chromosomes in excess of the basic complement as "supernumerary." He distinguished between those that arose by nondisjunction and others derived by fragmentation. Chromosomes in excess of the basic "A" complement that do not pair with A chromosomes and have certain other characteristics are more often referred to as "B" rather than "supernumerary" or "accessory" chromosomes. Chromosomes in excess of the basic complement are generally smaller than the A chromosomes, do not pair with them but can pair with each other, and often are more heterochromatic than the A chromosomes (Soltis 1983).

The number of supernumerary chromosomes may vary in the same plant, e.g., *Poa trivialis* L.(Bosemark 1957) or in different plants of the same population, e.g., *Xanthisma texanum* DC (Semple 1974). In *Clarkia unguiculata* Lindley, the frequency of individuals with supernumeraries varied from 0 to 79% in different populations, and, in one population, varied significantly in different years (Mooring 1960).

In some species, supernumerary chromosomes can be transmitted or increased in number, as in several grass species (e.g., *Festuca arundinacea* Schreber[Bosemark 1957], or in *Clarkia unguiculata* [Mooring 1960]). Rosato et al. (1996) reported that the transmission of B chromosomes in wild races of maize was under genetic control.

Whether these extra chromosomes are genetically inert, parasitic, or of some adaptive value is unclear, and may well depend on the species studied. Adaptive effects of supernumerary chromosomes are known or surmised; for example, Bosemark's (1956) study of *Festuca pratensis* Hudson found a correlation between the clay content of the soil in most Swedish provinces and the frequency of accessory chromosomes. The number of species reported to carry these extra chromosomes has increased sharply in the last 50 yr; about 2000 are known in many taxonomic groups of animals and flowering plants (see Palestis et al. 2004).

Background of Present Study

Eriophyllum lanatum (Pursh) Forbes and *E. confertiflorum* (DC.) A. Gray are polyploid complexes (Mooring 1975, 1994, 2001). *Eriophyllum lanatum* is a short-lived, woody-based, herbaceous perennial; *E. confertiflorum* var. *confertiflorum* is a subshrub. Both are highly self-incompatible. *Eriophyllum lanatum* is widely distributed in western North America from 5 to 3500 m; *E. confertiflorum* var. *confertiflorum* occurs from central California to adjacent Baja California from 5 to 3000 m.

Artificial hybridizations show barriers to interbreeding in both species complexes. Those in *E. confertiflorum* var. *confertiflorum* are weaker; consequently, the races are harder to delimit (Mooring 1994). Interbreeding barriers in *E. lanatum* are stronger; the 10 "varieties" of *E. lanatum* are geographic subspecies (Mooring 2001). Artificial hybrids have been obtained between *E. confertiflorum* var. *confertiflorum*

and all varieties of *E. lanatum* (Mooring 2001 and unpublished). Natural hybrids between *E. lanatum* and *E. confertiflorum* var. *confertiflorum* are infrequently encountered (Constance 1937; Mooring 1994). *Eriophyllum latilobum* Rydb. may be a product of such interspecific hybridization (Constance 1937; Munz 1959).

My report is an offshoot of long-term biosystematic studies of *Eriophyllum lanatum* (Mooring 1975, 2001) and *E. confertiflorum* (Mooring 1994). Those studies focused on the distribution of cytotypes and on barriers to interbreeding at the diploid level. The supernumerary chromosomes in both species presented interesting problems, but time and space requirements prevented further study.

The supernumerary chromosomes of *Eriophyllum lanatum* and of *E. confertiflorum* var. *confertiflorum* are in the size range of the smaller members of the basic complement. They do not seem to differ from the A chromosomes in appearance or behavior. With one apparent exception, they do not pair with an A chromosome. Thus, they resemble the supernumerary chromosomes of *Clarkia unguiculata* (Lewis 1951; Mooring 1960). Lewis (1951) believed that these extra chromosomes originated as trisomics.

The distribution and frequency of supernumerary chromosomes, especially in *E. lanatum*, suggest an adaptive role or meiotic drive, or both. Artificial hybridizations have shown that supernumeraries could be transmitted, but have not documented the frequency of transmittal (Mooring 2001).

Thus, in 2000, I began reciprocal crosses in *E. lanatum*: 8 II × 8 II + one supernumerary chromosome and 8 II × 8 II + two supernumerary chromosomes. I present my findings about both species in one report because the species are closely related and the results of each study are similar. The purpose of this paper is to report the frequency, geographic distribution, and transmission of supernumerary chromosomes in *E. lanatum, E. confertiflorum* var. *confertiflorum*, and their putative hybrid derivatives.

Materials and Methods

Species

Most of the plants used in this study were grown from fruits collected from natural populations; a few were transplants from these populations. The location of the *Eriophyllum lanatum* and *E. confertiflorum* var. *confertiflorum* natural populations are given in Mooring (2001) and Mooring (1994), respectively.

Treatments

Fruits were germinated in vermiculite or in vermiculite-soil mixtures. Seedlings were potted in "UC Mix" soil in an unheated Santa Clara University greenhouse.

Meiotic Analyses

Young capitula were fixed in 1:3 acetic ethanol or, rarely, in 1:3:6 acetic-chloroform-ethanol. Quickly putting collections in the refrigerator or an ice-filled cooler usually improved fixation (Anderson 1996). Beek's (1955) technique often provided clearer preparations. Most meiotic analyses were of diakinesis or first metaphase stages of microsporocytes squashed in acetocarmine and examined with a phase contrast microscope. Squashing anthers in 1% aceto-orcein instead of aceto-carmine often resulted in more darkly stained chromosomes. Voucher specimens have been deposited in the Santa Clara University Herbarium (SACL).

In this study, chromosomes in excess of the basic complement of *Eriophyllum lanatum* and *E. confertiflorum* var. *confertiflorum* are called supernumerary chromosomes rather than B chromosomes or accessory chromosomes. Because the *Eriophyllum* supernumerary chromosomes were morphologically indistinguishable from the chromosome of the basic complement ("A" chromosomes) at meiosis, I did not distinguish between A and supernumerary chromosomes in reporting meiotic configurations. The letter "I" is used to refer to an unpaired chromosome. Fragment chromosomes were also present, and are called fragment chromosomes.

Artificial Hybridizations

All hybridizations were performed in a pollinator-free greenhouse. The plants were separated by at least 30 cm. Capitula were rubbed together over 2–8 d.

Pollen Fertility Estimates

Fresh pollen grains were stained overnight in cotton blue-lactophenol. Estimates rest on 300 grains per sample. Each plant was sampled on two different days.

Results

Viability of Plants with Supernumerary Chromosomes

Plants with supernumerary chromosomes could be detected only by meiotic analysis. Pollen fertility varied widely in plants with and without extra chromosomes, but no significant differences were found.

Number of Supernumerary Chromosomes per Plant

I found one to four supernumerary chromosomes in *Eriophyllum lanatum*; and one, two, or

six supernumerary chromosomes in *E. confertiflorum* var. *confertiflorum*; and two in *E. latilobum*, a putative *E. lanatum* × *E. confertiflorum* var. *confertiflorum* hybrid (Tables 1 and 2).

Meiotic Configurations

In *E. lanatum*, diploids not derived from artificial hybridizations, one plant formed 8 II + 1 I in most microsporocytes, and 7 II + 1 III in others. The 7 II + 1 III configuration, if due to a chiasma rather than sticky chromosomes, suggests that in this instance a supernumerary can pair with A chromosomes. In all other such diploids, those with one supernumerary formed 8 II + 1 I. In a few cells scored as having 8 II + 1 I, the I divided at first metaphase, and 9 + 9 separations occurred in first anaphase cells. Conspicuously lagging chromosomes in first or second division were rare. Most plants with two supernumeraries formed 8 II + 2 I or 9 II. The single plant with 19 chromosomes formed 9 II + 1 I. One of the two plants with 20 chromosomes formed 10 II exclusively, the other variously 10 II, 9 II + 2 I, and, in a few cells, 8 II + I IV (Table 1).

In contrast to diploids not derived from artificial hybridizations, those derived from artificial hybridizations often formed variable meiotic configurations (Table 3). Notable among crosses producing progeny with variable meiotic configurations was Cross 7 in Table 4 between an 8 II + 1 I seed parent and an 8 II pollen parent. It produced two progeny with variable meiotic configurations. One formed 8 II + 1 I or 7 II + 3 I; the other formed 8 II + 1 I, 8 II + 2 I , 7 II + 3 I, and 7 II + 4 I.

In *E. lanatum* tetraploids, plants with one supernumerary formed 16 II + 1 I; those with two supernumeraries 16 II + 2 I or 17 II, or exclusively 17 II (Table 1).

In *E. confertiflorum* var. *confertiflorum*, diploids formed 8 II + 1 I if one supernumerary was present. One plant with two supernumeraries consistently formed 9 II. Other plants with more than one supernumerary formed 8 II + 2 or 3 I. Tetraploids formed 16 II + 1 I if one supernumerary was present but invariably or frequently formed 17 II if two were present, and 19 II when six were present (Table 2).

The single plant of *E. latilobum* with supernumeraries formed 16 II + 2 I.

Frequency of Supernumerary Chromosomes in *E. lanatum*

The overall frequency of plants and populations with supernumerary chromosomes was 12% (54/459) and 14% (42/293), respectively. Supernumerary chromosomes were not found in the total of 42 plants examined in vars. *croceum, hallii, lanceolatum*, and *obovatum* (Table 1). The frequency of supernumeraries in diploid, tetraploid, hexaploid, and octoploid plants of *E. lanatum* was, respectively, 13% (41/328), 10% (10/103), 0% (0/16), and 18% (2/11). Tetraploids with supernumerary chromosomes appeared limited to vars. *achillaeoides* and *leucophyllum*, and octoploids with supernumerary chromosomes to var. *integrifolium* (Table 1).

The frequency of supernumerary chromosomes varied among populations and varieties, from 34% for individuals and 31% for populations in var. *lanatum* to 4% and 7% in var. *arachnoideum*.

Frequency of Supernumerary Chromosomes in *E. confertiflorum* var. *confertiflorum*

The overall frequency of plants and populations with supernumerary chromosomes was 13% (24/180) and 15% (20/133), respectively. One plant had a fragment chromosome; the rest had normal-sized supernumerary chromosomes. The frequency of supernumerary chromosomes in diploid, tetraploid, hexaploid and octoploid populations was, respectively, 9%(6/69), 22% (13/60), 0% (0/1), and 0% (0/2). One population (*143*) was mixed, having a diploid with two supernumeraries and two tetraploids with none (Table 2). Only 39% of the diploid populations had supernumeraries, compared to 74% in *E. lanatum*.

Supernumerary Chromosomes in Putative *E. confertiflorum* var. *confertiflorum* × *E. lanatum* derivatives

Eriophyllum latilobum consists of two populations along San Mateo Creek in San Mateo County, California. Individuals formed 16 II except for one that formed 16 II + 2 I. The other putative *E. confertiflorum* var. *confertiflorum* × *E. lanatum* hybrids were tetraploids and hexaploids with one or two supernumerary chromosomes, forming 16 II + 1 I, 17 II, 24 II + 1 I, or 25 II. The frequency of individuals and of populations with supernumerary chromosomes was, respectively, 24% and 50%. The putative hybrid populations were restricted to an approximately 40 km strip in San Mateo and adjacent Santa Clara Counties, California (Table 2).

Transmission of Supernumerary Chromosomes in Artificial Intervarietal and Interspecific Hybridizations in *E. lanatum* and *E. confertiflorum* var. *confertiflorum*

The chromosome number of 13 of the 30 parents in 17 hybridizations (Table 3) was known; the other parents were assumed to form

8 II because representatives of the parental populations formed 8 II. The crosses in Table 3 are divided into four sections and are numbered to facilitate describing the results. Supernumerary chromosomes were transmitted in all crosses.

In Section 1, where the chromosome number of both parents was known, transmission of one supernumerary failed in one of the parents in Cross 1. One supernumerary was transmitted by the seed parent in Cross 2 and by the pollen parent in Cross 3.

In Section 2, where the chromosome number of the seed parent was known, and transmission was through the seed parent, two supernumeraries in Cross 4 and one in Cross 5. In Crosses 6 and 7, transmission probably occurred through the pollen parent, because the seed parent formed 8 II, and supernumeraries had been observed in populations *204* and *205* from which the pollen parents came (Table 1). The origin of supernumeraries in Cross 8 was uncertain. The seed parent formed 8 II, and although supernumeraries were not observed in the pollen parent population (*38*), the single plant examined in the progeny formed 8 II + 1 I or 7 II + 3 I.

In Section 3, (chromosome number of pollen parent known) the results paralleled those in Section 2. Transmission was through the pollen parent in Crosses 9 and 10, two supernumeraries in Cross 9 and one in Cross 10. In Cross 11, the fragment and supernumerary probably came from the seed parent, S184-1, because supernumeraries occurred in Population 184 (Table 1). The source of the supernumerary in Cross 12 was unknown because supernumeraries were not found in the parental populations.

In Section 4, chromosome numbers were unknown for the parents. Presumably the parents formed 8 II as in their parental populations. The source or sources of the supernumeraries in the progenies was not known (Table 3). All but Cross 15 were either interspecific or intervarietal, and were often between geographically distant populations.

Frequency of Transmission of *E. lanatum* Supernumerary Chromosomes in Artificial Hybridizations

In pre-2000 hybridizations, how frequently supernumeraries were transmitted was unknown because usually only one plant per cross was analyzed (Table 3). Attempts to use reciprocal crosses to estimate transmission frequencies were only partly successful because low percentage germination or failure to flower resulted in only two of five combinations being reciprocal.

The crosses in Table 4 are numbered to facilitate describing the results. The meiotic configuration of the seed parent is known in Crosses 1–3, and both parents are known in Crosses 4–7. Transmission of one or two supernumerary chromosomes occurred in five of the six progeny in Cross 1, and in 7 of 10 progeny in Cross 2. In Cross 3, the chromosome number of the pollen parent is not known, and the population that furnished it had plants that formed 8 II + 1 I as well as 8 II. If the pollen parent formed 8 II, the supernumerary in the seed parent was transmitted to 9 of the 17 progeny, and multiplied in one of them. A fragment chromosome was also transmitted to three other plants, probably from the pollen parent. Crosses 4 and 5 were reciprocal; the supernumerary chromosome was transmitted when *S338-4* was the seed parent but not when it was the pollen parent. However, failure of transmittal through the pollen may be a matter of chance; the progeny consisted of only two plants. Crosses 6 and 7 are reciprocal. Transmission through the pollen parent occurred in 7 of the 18 progeny (39%), compared to 9 of the 14 progeny (64%) for the seed parent.

Pollen fertility figures for progeny with and without supernumeraries did not differ significantly (Table 4).

Nonrandom Geographic Distribution of *E. lanatum* Populations with Supernumerary Chromosomes

Six regions had one to five populations with a high frequency of supernumerary chromosomes. Along the Snake River in Idaho and Oregon, 11 of the 16 plants in five diploid var. *lanatum* populations had one or two supernumeraries. In Trinity County, California, each of three diploid var. *grandiflorum* populations was represented by a plant with two supernumerary chromosomes. In Colusa and Lake Counties, California, two diploid and two tetraploid var. *achillioides* populations were represented by single plants with one supernumerary or one fragment chromosome. In southwestern Oregon (Jackson, Josephine, and Douglas Counties), four of the six plants in tetraploid var. *achillioides* Populations *335* and *62*, and var. *leucophyllum* Populations *18* and *337* had one or two supernumerary chromosomes. Also, all four plants in diploid Population *338*, an *achillioides-leucophyllum* intermediate, had one or two supernumeraries. Two diploid populations of var. *integrifolium* had high frequencies of plants bearing supernumerary chromosomes. In Adams County, Washington, four of five plants in Population *265* had one to three extra chromosomes. In Elko County, Nevada, each of the single plants in Populations *250* and *251* had four extra chromosomes (Table 1).

TABLE 1. SUPERNUMERARY CHROMOSOMES IN *ERIOPHYLLUM LANATUM* POPULATIONS. Locations within counties are approximate. An asterisk indicates that a univalent was seen to divide at Metaphase 1, two asterisks that 9 + 9 disjunctions were seen to occur. The numbers following a taxon name show, respectively, the frequency of individuals and populations with supernumeraries.

Taxa/Location	Population	Meiotic configuration		Number of plants: With that configuration	Number of plants: Analyzed
Var. *achillioides* (8/85 = 9%; 8/61 = 13%)					
CA, Lake Co., Kelseyville	*120*	8 II + fragment		1	1
Lake Co., Clear Lake	*127*	8 II + 1 I, 7 II + 1 III		1	1
Siskiyou Co., Dorris	*111*	8 II + 1 I**		1	2
Colusa Co., Leesville	*183*	16 II + 1 I		1	1
Lake Co., Clear Lake	*132*	16 II + 1 I		1	1
Shasta Co., Fall River Mills	*153*	16 II + 2 I or 17 II		1	1
OR, Jackson Co., Central Point	*335*	17 II		1	1
Josephine Co., Selma	*62*	16 II + 1 I		1	1
			Total	8 (89%)	9
Var. *arachnoideum* (1/24 = 4%; 1/14 = 7%)					
CA, San Mateo Co., Woodside	*361*	8 II + 1 I	Total	1 (50%)	2
Var. *croceum* (0/14; 0/6)					
Var. *grandiflorum* (5/89 = 6%; 5/57 = 9%)					
CA, Calaveras Co., Murphy's	*76*	8 II + 1 I		1	2
El Dorado Co., Diamond Springs	*179*	9 II or 8 II + 2 I		1	1
Trinity Co., Trinity Center	*174*	9 II or 8 II + 2 I		1	1
Trinity Center	*184*	9 II		1	1
Trinity Center	*221*	8 II + 2 I or 9 II		1	1
			Total	5 (83%)	6
Var. *hallii* (0/3; 0/1)					
Var. *integrifolium* (16/100 = 16%; 13/60 = 22%)					
CA, Mono Co., Sonora Pass Summit	*114*	8 II + 1 I		1	2
ID, Blaine Co., Ketchum	*257*	8 II + 1 I		1	2
Custer Co., Stanley	*256*	8 II + 1 I		1	2
Owyhee Co., Riddle	*252*	8 II + 1 I		1	1
NV, Elko Co., Elko	*250*	10 II		1	1
Elko Co, Mountain City	*251*	10 II, 9 II + 2 I, 8 II + 1 IV in a few cells		1	1
OR, Deschutes Co., La Pine	*108*	8 II + 1 I		1	1
Wheeler Co., Antone	*271*	8 II + 2 I		1	1
WA, Adams Co., Ritzville	*265*	8 II + 1 I or 9 II		1	5
		8 II + 1 I to 7 II + 3 I		1	
		8 II + 1 I		1	
		9 II + 1 I		1	
WY, Fremont Co., Dubois	*56*	8 II + 1 I		1	1
Teton Co., Moran	*55*	8 II + 1 I		1	1
OR, Wasco Co., The Dalles	*104*	32 II + 1 I		1	1

TABLE 1. CONTINUED.

Taxa/Location	Population	Meiotic configuration		Number of plants: With that configuration	Number of plants: Analyzed
WA, Klickitat Co., The Dalles Dam	*102*	33 II		1	1
			Total	16 (80%)	20
Var. *lanatum* (11/32 = 34%; 5/16 = 31%)					
ID, Idaho Co., Harpster	*30*	8 II + 2 I		1	1
Washington Co., Beggs	*204*	8 II + 1 I		1	3
		8 II + 2 I		1	
Washington Co., Brownlee Dam	*325*	8 II + 2 I		2	4
		8 II + 2 I to 7 II + 4 I		1	
OR, Baker Co., Oxbow Dam	*205*	8 II + 1 I		2	3
Oxbow Dam	*324*	8 II + 2 I		2	5
		8 II + 1 I		1	
			Total	11 (69%)	16
Var. *lanceolatum* (0/12; 0/8)					
Var. *leucophyllum* (6/37 = 16%; 6/29 = 21%)					
OR, Douglas Co., Glide	*18*	16 II + 1 I		1	2
Douglas Co., Azalea	*337*	16 II + 2 I		1	2
Marion Co., Silverton	*94*	8 II + 2 I or 9 II		1	1
Multnomah Co., Shepperd's Dell	*355*	8 II + 2 II*		1	1
WA, Cowlitz Co., Kalama River	*172*	9 II or 8 II + 2 I		1	1
San Juan Co., Orcas Island	*239*	8 II + 1 I		1	2
			Total	6 (67%)	9
Var. *obovatum* (0/13; 0/7)					
INTERGRADES BETWEEN VARIETIES (7/50 = 14%; 4/34 = 12%)					
Var. *achillioides*-var. *arachnoideum* (1/12 = 8%; 1/9 = 11%)					
CA, Napa Co., St. Helena	*229*	17 II		1	1
Var. *achillioides*-var. *grandiflorum* (1/17 = 6%; 1/11 = 9%)					
CA, Glenn Co., Stonyford	*195*	17 II or 16 II + 2 I		1	2
Var. *achillioides*-var. *leucophyllum* (4/5 = 80%; 1/2 = 50%)					
OREGON, Douglas Co., Dillard	*338*	8 II + 1 I		3	4
		8 II + 2 I or 9 II			
Var. *arachnoideum*-var. *grandiflorum* (0/2; 0/2)				1	
Var. *grandiflorum-integrifolium* (1/3 = 33%; 1/2 = 50%)					
CA, Nevada Co., Emigrant Gap	*332*	16 II + 1 I		1	3
Var. *grandiflorum*-var. *lanceolatum* (0/1; 0/1)					
Var. *integrifolium*-var. *lanatum* (0/10; 0/7)					
TOTAL: (54/459 = 12%; 42/293 = 14%)					

TABLE 2. SUPERNUMERARY CHROMOSOMES IN POPULATIONS OF *ERIOPHYLLUM CONFERTIFLORUM* VAR. *CONFERTIFLORUM*, *E. LATILOBUM*, AND PUTATIVE *ERIOPHYLLUM CONFERTIFLORUM* VAR. *CONFERTIFLORUM* × *E. LANATUM* HYBRID DERIVATIVES. Regional and county names are bolded. Locations within counties are approximate. An asterisk indicates that a univalent was seen to divide at Metaphase 1. The numbers following the taxon name show, respectively, the frequency of individuals and populations with supernumerary chromosomes. The numbers following a county name show the frequency of populations with supernumeraries. Counties, all in California, are arranged in north to south order, as are populations in them. Percentages are rounded.

Location	Population	Meiotic configuration	Number of plants: With that configuration	Number of plants: Analyzed
Eriophyllum confertiflorum* var. *confertiflorum (24/180 = 13%; 20/133 = 15%)				
		South Coast Ranges		
Alameda (1/4), Arroyo Mocho	*16*	16 II + 1 I	1	1
San Mateo (3/7), Hillsborough	*143*	8 II + 2 I*	1	2
Montebello Ridge	*22*	16 II + 1 I	1	2
Portola State Park	*142*	17 II, 16 II + 2 I	1	2
Santa Clara (3/15), Loma Prieta	*10*	16 II + 2 I	1	1
Loma Prieta	*11*	17 II	1	2
Mt. Hamilton	*18*	16 II + 1 I	1	1
Monterey (4/13), Del Monte	*7*	16 II + 1 I	1	1
Carmel Valley	*25*	17 II	2	4
		19 II	1	
Big Sur	*107*	8 II + 1 I	1	1
Lucia	*36*	16 II + 1 I	1	2
San Benito (1/10), Pinnacles N. M.	*136*	17 II	1	1
			Total 14 (70%)	20
		Transverse Ranges		
Santa Barbara (2/9), Lompoc	*67*	16 II + 1 I	1	2
New Cuyama	*150*	17 II	2	3
			Total 3 (60%)	5
		Peninsular Ranges		
San Diego (2/8), Escondido	*61*	9 II	1	2
Vista	*147*	8 II + 1 I	1	1
			Total 2 (67%)	3
		Sierra Nevada		
Calaveras (1/1), Mokelumne	*85*	16 II + 1 I	1	1
Mariposa (1/8), El Portal	*127*	8 II + 1 I	1	1
Tulare (1/5), Mineral King Road	*79*	8 II + 3 I	1	1
Kern (1/9), Wofford Heights	*77*	8 II + 1 fragment	1	2
	77	8 II + 2 I	1	
			Total 5 (100%)	5
Eriophyllum latilobum (1/9 = 11%; 1/2 = 50%)				
San Mateo, San Mateo Creek dam	*5*	16 II + 2 I	1 (33%)	3
Putative natural hybrids, *E. lanatum* var. *arachnoideum* × *E. confertiflorum* var. *confertiflorum* (6/25 = 24%; 4/8 = 50%)				
San Mateo, Alpine Road	*9*	16 II + 1–2 I	1	5
Black Mountain	*1*	24 II + 1 I	2	5
		25 II	1	
Borel Hill	*11*	17 II	1	3
Santa Clara, Montebello Ridge	*6*	25 II	1	1
			Total 6 (43%)	14

Nonrandom distribution of *E. confertiflorum* var. *confertiflorum* Tetraploid Populations with Supernumerary Chromosomes

Although the overall ratio of *E. confertiflorum* var. *confertiflorum* diploid to tetraploid populations was 69 to 60, tetraploid populations with supernumeraries outnumbered diploid ones 13 to 6. That ratio rose to 8 to 2 in Monterey, Santa Clara, and San Mateo Counties, California. Only two populations with supernumeraries were found south of Santa Barbara County. They were diploids only 16 km apart, in San Diego County (Table 2).

Discussion

Frequency of Supernumerary Chromosomes Probably Underestimated

I examined only one or two plants in most populations. Larger samples likely would have shown more populations with supernumeraries and different frequencies of supernumeraries in the populations.

Hypotheses for Presence of Supernumerary Chromosomes in *E. lanatum*

Various hypotheses have been proposed to account for supernumerary chromosomes in other species, including adaptive value and meiotic drive that could perpetuate extra chromosomes even if they had deleterious effects. I have no information about *E. lanatum* that would support or discount adaptive value or meiotic drive. Supernumerary chromosomes, however, can be transmitted in *E. lanatum* varieties (Table 3, 4). Also, artificial hybridizations of diploids representing vars. *achillioides, grandiflorum, integrifolium*, and *lanatum* show that barriers to interbreeding are comparatively low (Mooring 2001, Table 7).

Natural hybridization between chromosomally differentiated populations could lead to gametes with extra chromosomes. The meiotic configurations in the progenies of Crosses 8, 16, and 17 (Table 3) suggest chromosomal restructuring accompanied by the presence of supernumerary chromosomes. Chromosomal restructuring is evident from many other artificial hybridizations between diploids in *E. lanatum* (Mooring 2001).

Except for the Elko County, Nevada, var. *integrifolium* population, all others with a high frequency of supernumerary chromosomes occurred where different varieties meet. The Adams County, Washington, var. *integrifolium* population is adjacent to var. *lanatum* populations. Variety *integrifolium* populations surround the var. *lanatum* populations along the Snake River. Oregon has diploid populations intermediate between the two varieties (Mooring 2001). Artificial hybridizations between diploids show that barriers to interbreeding are low. Mean percentage pollen fertility of *integrifolium* × *lanatum* progeny was 60 ± 23% (Mooring 2001, Table 7).

The var. *grandiflorum* populations in Trinity County, California, are in a region where vars. *achillioides, grandiflorum*, and *lanceolatum* meet; some populations there are intermediate. Diploid progenies from artificial *achillioides* × *grandiflorum, achillioides* × *lanceolatum*, and *grandiflorum* × *lanceolatum* hybridizations have mean pollen fertilities of, respectively, 57 ± 18%, 66 ± 16%, and 68 ± 16% (Mooring 2001, Table 7).

Similarly, the var. *achillioides* cluster in Lake and Colusa Counties, California, occurs where vars. *achillioides, arachnoideum*, and *grandiflorum* merge. Intergrades are numerous (Mooring 2001). Diploid progenies from vars. *achillioides* × *arachnoideum, achillioides* × *grandiflorum*, and *arachnoideum* × *grandiflorum* artificial hybridizations had, respectively, pollen fertilities of 74 ± 8%, 57 ± 18%, and 51 ± 16% (Mooring 2001, Table 7).

Varieties *achillioides* and *leucophyllum* are sympatric in southwestern Oregon. (Variety *achillioides* populations in northern California and southwestern Oregon differ markedly from the southern populations. Variety *ternatum* Greene has been proposed to recognize them.) Differentiating between var. *achillioides* (possibly also var. *ternatum*) and var. *leucophyllum* becomes difficult or impossible, notably in Douglas County, Oregon. Artificial hybridizations between Douglas County Population *338* and two var. *leucophyllum* populations produced diploid progenies whose mean pollen fertility was 78% ± 16 and 81% ± 13 (Mooring, unpublished).

Hypotheses for Nonrandom Distribution of *E. confertiflorum* var. *confertiflorum* Tetraploid Populations with Supernumerary Chromosomes

At least three hypotheses can be made for the nonrandom distribution of *E. confertiflorum* var. *confertiflorum* tetraploid populations with supernumerary chromosomes, especially those in Monterey, Santa Clara, and San Mateo Counties (Table 2): 1) supernumerary chromosomes are adaptive, 2) meiotic drive exists, and 3) local climatic or edaphic conditions affect meiosis and thereby lead to gametes with extra chromosomes. These hypotheses are not mutually exclusive. Two other explanations peculiar to polyploids are: 1) tetraploids tolerate supernumeraries better than diploids, and 2) some plants described as having supernumerary chromosomes may be aneuploids generated by neopolyploids (see Ramsey and Schemske 2002, pp. 601–607).

TABLE 3. ARTIFICIAL INTERVARIETAL AND INTERSPECIFIC HYBRIDIZATIONS IN *ERIOPHYLLUM LANATUM* AND *E. CONFERTIFLORUM* VAR. *CONFERTIFLORUM* THAT PRODUCED PROGENY WITH SUPERNUMERARY CHROMOSOMES. Seed parent is listed first. Only one plant in each progeny was examined meiotically. Each of the 17 crosses is numbered. Bolded chromosome counts are those known for the parent, unbolded those known for the population that furnished it.

Parental taxa and location	Parents	Meiotic configuration
SECTION 1. CHROMOSOME NUMBER OF BOTH PARENTS KNOWN		
Eriophyllum confertiflorum var. *confertiflorum* × *E. lanatum* var. *lanatum*, CALIFORNIA, Mariposa × OREGON, Baker		
1. Eagle Peak × Oxbow Dam	*S127-2* **(8 II + 1 I)** × *S324-7* **(8 II + 1 I)**	8 II + 1 I
Eriophyllum confertiflorum var. *confertiflorum* × *E. lanatum* var. *croceum*, CALIFORNIA, Mariposa × Fresno		
2. Eagle Peak × Badger	*S127-2* **(8 II + 1 I)** × *S309-22* **(8 II)**	8 II + 1 I to 6 II + 5 I
Eriophyllum lanatum var. *obovatum* × var. *lanatum*, CALIFORNIA, San Bernardino × OREGON, Baker		
3. Running Springs × Oxbow Dam	*S289-14* **(8 II)** × *S324-3* **(8 II + 1 I)**	8 II + 1 I (I frequently divides at M1)
SECTION 2. CHROMOSOME NUMBER OF SEED PARENT KNOWN		
Eriophyllum lanatum var. *integrifolium* × var. *arachnoideum*, WASHINGTON, Adams × CALIFORNIA, Mendocino		
4. Ritzville × Elk	*S265-4A* **(8 II + 2 I)** × *S212-1* (8 II)	9 II, occasional 8 II + 2 I
Eriophyllum confertiflorum var. *confertiflorum* × *E. confertiflorum* var. *confertiflorum* CALIFORNIA, Mariposa × Santa Cruz		
5. Eagle Peak × Bonny Doon	*S127-2* **(8 II + 1 I)** × *20* (8 II)	8 II + 1 I
Eriophyllum lanatum var. *achillioides* × var. *lanatum*, CALIFORNIA, Yolo, × IDAHO, Washington		
6. Winters × Brownlee Dam	*S150-2* **(8 II)** × *S204-3* (8 II, 8 II + 1 or 2 I)	8 II + 1 I
Eriophyllum lanatum var. *integrifolium* × var. *lanatum*, OREGON, Union × OREGON, Baker		
7. Elgin × Oxbow	*S267-33* **(8 II)** × *S205-34* (8 II, 8 II + 1 I)	8 II + 1 I
Eriophyllum lanatum var. *lanceolatum* × var. *achillioides*, CALIFORNIA, Humboldt × CALIFORNIA, Santa Clara		
8. Slate Creek × Loma Prieta	*280-3* **(8 II)** × *38-11* (8 II)	8 II + 1 I, 7 II + 3 I
SECTION 3. CHROMOSOME NUMBER OF POLLEN PARENT KNOWN		
Eriophyllum lanatum var. *integrifolium* × var. *lanatum*, WYOMING, Yellowstone National Park × IDAHO, Washington		
9. Tower Junction × Brownlee Dam	*S58-1* (8 II) × *S204-1* **(8 II + 2 I)**	8 II + 2 I or 9 II
Eriophyllum lanatum var. *arachnoideum* × *Eriophyllum confertiflorum* var. *confertiflorum*, CALIFORNIA, Mendocino × Los Angeles		
10. Elk × Vincent	*S212-1* (8 II) × *S74-4B* **(8 II + 1 I)**	8 II + 1 I
Eriophyllum lanatum var. *grandiflorum* × var. *grandiflorum*, CALIFORNIA, Trinity × CALIFORNIA, El Dorado		
11. Trinity Center × Coloma	*S184-1* (8 II) × *S187-2* **(8 II)**	8 II + 1 I + 1 fragment

TABLE 3. CONTINUED.

Parental taxa and location	Parents	Meiotic configuration
Eriophyllum lanatum var. *arachnoideum* × var. *leucophyllum*, CALIFORNIA, San Mateo × OREGON, Multnomah		
12. Woodside × Shepperd's Dell	*330-1* (8 II) × *S355-4* **(8 II)**	8 II + 1 I
SECTION 4. CHROMOSOME NUMBER OF NEITHER PARENT KNOWN, THAT OF PARENTAL POPULATION KNOWN		
Eriophyllum lanatum var. *achillioides* × var. *hallii*, CALIFORNIA, Santa Barbara × CALIFORNIA, Contra Costa		
13. Mt Diablo × New Cuyama	*S306sib* (8 II) × *S7-3* (8 II)	8 II + 1 I
Eriophyllum lanatum var. *arachnoideum* × var. *obovatum*, CALIFORNIA, San Mateo × CALIFORNIA, Kern		
14. Woodside × Greenhorn Summit	*330-2* (8 II) × *322-17* (8II)	8 II + 1 fragment
Eriophyllum confertiflorum var. *confertiflorum* × *Eriophyllum confertiflorum* var. *confertiflorum*, CALIFORNIA, San Diego × Santa Cruz		
15. San Diego × Bonny Doon	*S120-1* (8 II) × *20* (8 II)	8 II + 1 fragment
Eriophyllum lanatum var. *integrifolium* × var. *integrifolium*, WYOMING, Yellowstone National Park × IDAHO, Boise		
16. Tower Junction × Banks	*S58-4* (8 II) × *S158-8* (8II)	8 II + 1 I, occasional 6 II + 1 IV + 1 I
Eriophyllum lanatum var. *grandiflorum* × var. *leucophyllum*, CALIFORNIA, Tehama × WASHINGTON, Island		
17. Payne's Creek × Deception Pass	*S199-12* (8 II) × *237-1* (8 II)	6 II + 4 I most frequent, also 8 II, 7 II + 2 I, I sometimes divides, 7 II + 3 I, 6 II + 5 I, 5 II + 1 III + 1 I

Supernumerary Chromosomes and Dysploidy

In *Eriophyllum*, as presently constituted, base chromosome numbers are n = 4, 5, and 7 for the annual species and n = 8 for the perennial species. Two annual species have extra chromosomes. Counts for *E. wallacei* are 5 II + 0-1 I (Taylor 1967; Strother 1972, 1976; Johnson 1978), and 5 II + 0-3 B chromosomes (Johnson 1978). Counts for *E. pringlei* are 7 II + 0-1 centric fragment (Strother 1972, 1976), 8 II (Keil and Pinkava 1976), 7 II + 0-1 I and 7 II + 0-3 B chromosomes (Johnson 1978). Supernumerary chromosomes are also present in the perennial eriophyllums. *Eriophyllum lanatum* has one to four supernumerary chromosomes; *E. confertiflorum* var. *confertiflorum* has one, two, or six supernumerary chromosomes.

Grant (1981, pp. 358–360) referred to a base haploid chromosome number series of 8-7-( )-4-3 in *Eriophyllum* and *Pseudobahia* as an example of "descending aneuploidy" derived by unequal reciprocal translocations. (The symbol ( ) indicates missing intermediate numbers.) However, supernumerary chromosomes may also have been involved in the formation of the dysploid series. Supernumerary chromosomes might have become members of the A complement, especially if they are trisomics. Alternatively, extra chromosomes might be obtained by interspecific hybridizations. Lewis (1953) suggested that ascending dysploidy (x = 7, 8, and 9) in *Clarkia* may have involved the acquisition of supernumerary chromosomes or the occurrence of interspecific hybridizations. Lewis and Roberts (1956) described the origin of *Clarkia lingulata* (n = 9) from *C. biloba* (n = 8) by the addition of a tertiary trisomic.

It is interesting that base haploid chromosome numbers in the closely related genera *Eriophyllum, Syntrichopappus*, and *Pseudobahia* (Baldwin and Wessa 2000) form the dysploid series 8-7-6-5-4-3. Perhaps significantly, *P. heermannii* (Durand) Rydb. has three base haploid chromosome numbers and chromosomes in excess of the basic complement, $2n$ = 6 + 0–2 I, $2n$ = 8 + 0–1 I or 0–1 B, and $2n$ = 10 + 0–1 I (Johnson 2006). For the past three years, I have been maintained an artificial hybridization program in *Pseudobahia heermanni* to analyze meiosis, detect barriers to

TABLE 4. FREQUENCY OF SUPERNUMERARY CHROMOSOMES IN PROGENY FROM ARTIFICIAL HYBRIDIZATIONS IN *ERIOPHYLLUM LANATUM*. Seed parent is listed first. Bolded chromosome counts are those known for the parent, unbolded those known for the population that furnished the parent. State and county names are bolded. Locations within counties are approximate. The crosses are numbered to facilitate explanations. NCD = no chromosome number data; meiosis was not examined in that parent, and 8 II and 8 II + 1 I are known in that population. Figures in parentheses in progeny columns are pollen fertility percentages ± 1 SD.

Taxa, parental location, cross	2*n* number of chromosomes (and % pollen fertility of progeny)				
	16	17	17 + fragment	18	N
Var. *achillioides-leucophyllum* intermediate × **var. *leucophyllum***, OREGON, Douglas, Dillard × Wasco, Rowena					
1. *S338-6* (**8 II + 2 I**) × *S342-6* (8 II)	1 (89)	3 (66 ± 20)	0	2 (73 ± 6)	6
Var. *leucophyllum* × **var. *obovatum***, OREGON, Multnomah, Shepperd's Dell × CALIFORNIA, Kern, Greenhorn Summit					
2. *S355-6* (**8 II + 2 I**) × *322A-10* (8 II)	3 (29 ± 5)	3 (27 ± 2)	0	4 (27 ± 9)	10
Var. *achillioides-leucophyllum* intermediate × **var. *achillioides***, OREGON, Douglas, Dillard × CALIFORNIA, Napa, Calistoga					
3. *S338-4* (**8 II + 1 I**) × *118-2* (NCD)	4 (80 ± 11)	9 (71 ± 10)	3 (66 ± 10)	1 (67)	17
Var. *achillioides-leucophyllum* intermediate × **var. *achillioides***, OREGON, Douglas, Dillard × OREGON, Josephine, Galice					
4. *S338-4* (**8 II + 1 I**) × *S350-13* (**8 II**)	1 (51)	1 (52)	0	0	2
5. R	2 (75 ± 26)	0	0	0	2
Var. *achillioides* × **var. *achillioides***, CALIFORNIA, Napa, Calistoga					
6. *118-4* (**8 II**) × *118-5* (**8 II + 1 I**)	11 (85 ± 17)	7 (87 ± 11)	0	0	18
7. R	5 (74 ± 24)	9 (75 ± 37)	0	0	14

interbreeding, and see if the extra chromosomes can be transmitted. The extra chromosomes can be transmitted (Mooring unpublished).

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SUBSPECIFIC VARIATION IN THE WIDESPREAD BURL-FORMING *ARCTOSTAPHYLOS GLANDULOSA*

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ABSTRACT

The genus *Arctostaphylos* consists mostly of chaparral shrubs known by the common name manzanita, and one of the widest ranging of these is *A. glandulosa* Eastw., distributed from Baja California to Oregon. Particularly in the southern half of its range it exhibits complex patterns of morphological variation that have long presented taxonomic challenges. Phenetic analysis of morphological traits from over 1400 individuals from throughout the range were used to examine intra- and inter-population patterns of variation. Multivariate ordination and hierarchical cluster analysis were used to determine phenetic patterns linked with ecological and geographical distributions. These analyses suggest the hypothesis that this species comprises two lineages with a common origin but divergent in the presence or absence of glandularity: *A. glandulosa* Eastw. subsp. *glandulosa*, characterized by branchlets with long glandular hairs, scabrous or pubescent leaves, and nascent inflorescences with mostly foliaceous bracts; and **A. glandulosa** Eastw. subsp. **cushingiana** (Eastw.) Keeley, Vasey and Parker comb. nov., with non-glandular tomentose branchlets, glabrate or pubescent leaves and either foliaceous or short deltoid bracts. Populations dominated by one or the other of these morphotypes occur throughout the range and tend to be separated by elevation or distance from the coast, although mixed populations occur where these taxa come together.

Two other glandular subspecies are named here. One is **A. glandulosa** Eastw. subsp. **leucophylla** Keeley, Vasey and Parker, subsp. nov., with intensely glaucous leaves and commonly with foliaceous bracts. A second glandular subspecies is **A. glandulosa** Eastw. subsp. **atumescens** Keeley, Vasey & Parker, subsp. nov., a narrowly distributed Baja California endemic similar to the nominate subspecies except that it lacks a basal burl and does not resprout after fire.

Of the non-glandular tomentose taxa, in addition to *A. glandulosa* subsp *cushingiana*, several others are also recognized. One is *A. glandulosa* Eastw. subsp. *crassifolia* (Jepson) Wells, a well established coastal San Diego endemic recognized by darker and thicker leaves and smaller and flatter fruits. Another is a newly described taxon **A. glandulosa** Eastw. subsp. **erecta** Keeley, Vasey & Parker, subsp. nov., an endemic to northern Baja California recognized by the erect nascent inflorescenses. Two others have glabrate leaves and highly reduced deltoid often marcescent bracts; *A. glandulosa* subsp. *adamsii* (Munz) Wells, which has intensely glaucous leaves and is distributed from interior Riverside Co. south, and **A. glandulosa** Eastw. subsp. **gabrielensis** (Wells) Keeley, Vasey and Parker comb. nov., which has bright lustrous green leaves and greater fusion of nutlets, and is distributed from the interior San Gabriel Mountains of Los Angeles Co. north to the Sierra Madre Mountains of Santa Barbara Co. All non-glandular plants with long setose or villous hairs are **A. glandulosa** Eastw. subsp. **mollis** (Adams) Wells. This taxon includes plants with foliaceous as well as reduced bracts and is distributed throughout the Transverse Ranges from Santa Barbara to San Bernardino counties, with some outlying populations further south. This taxon shows a marked tendency for reduced stomatal densities on the upper leaf surface in the westernmost populations. Although all of the *A. glandulosa* taxa described here are known from allopatric populations, intergradations of these closely related taxa occur and thus some populations reflect a mixture of traits and can not be assigned a unique name of practical value.

Key Words: chaparral, evolution, hybridization, introgression, latitude, subspecies, traits.

Arctostaphylos is a genus of shrubs whose center of diversity is in chaparral shrublands of the California floristic province. Currently 61 species and an additional 32 subspecies are recognized (Wells 2000a). Complex patterns of variation in this genus have been a challenge to taxonomists for more than a century. A number of factors contribute to this complexity. No fertility barriers are known between species in the genus and hybridization and introgression are suspected to occur between many species. There also is much infra-specific variation that has been treated in various ways, including varieties, subspecies, and formas.

One of the key life history differences between *Arctostaphylos* taxa is the response to fire and this has played an important role in the taxonomy of the genus. High intensity crown fires are a predictable feature of chaparral shrublands and most species in the genus produce dormant seed banks that are stimulated to germinate by chemicals from combustion products of fire (Keeley 1991). Some *Arctostaphylos* species are killed outright by fire and are entirely dependent on seed bank storage (Parker and Kelly 1989) and postfire germination in order to persist in fire-prone environments, and are known as obligate seeders (Keeley 1991). Other species couple postfire seedling recruitment with resprouting from a swollen burl or lignotuber at the base of the main stem (Fig. 1a), and these are known as facultative seeders. These burls, which are an important taxonomic character, are a normal ontogenetic stage and are apparent in seedlings after the first year (Fig. 1b). They potentially confer great longevity to genets capable of persisting through repeated fire cycles and expanding to form platform burls (Fig. 1c) and are an important taxonomic character.

The most widespread Californian *Arctostaphylos* species is the resprouting *A. glandulosa* Eastw. It is common in the coastal mountains from northern Baja California to southern Oregon but is absent from the Sierra Nevada. It is normally circumscribed as a tetraploid ($n = 26$) burl-forming species having isofacial leaves with roughly similar stomatal density on the upper and lower leaf surfaces, and small somewhat depressed globose fruits that comprise half a dozen nutlets variously fused and usually breaking apart into 2–5 segments. The species always possess some form of indument from puberulent to densely glandular hairy. Nascent inflorescence bracts range from linear foliaceous to highly reduced scale-like deltoid.

A number of factors have contributed to patterns of variation in *A. glandulosa*. The widespread distribution in diverse habitats has likely played some selective role in generating variation. Also, the burl-forming habit contributes to patterns of variation not generally seen in obligate seeding species. That is, obligate seeding species mix genes every fire-initiated generation and thus tend to homogenize population characteristics, whereas resprouting allows different morphotypes to persist indefinitely as clones, and thus increase morphological variation within populations. Also the burl forming habit may carry a cost in terms of migration during the marked climatic fluctuations, most recently during the late Quaternary (Axelrod 1950; Raven and Axelrod 1978; Wells 2000b; Rhode 2002), but the effect on patterns of variation are unexplored. Another potential factor is hybridization and introgression. Wells (2000a) speculated that *A. glandulosa* had hybridized with more than a dozen other species, although little morphological or molecular data exist to support this claim.

The most recent treatment of intra-specific variation in *A. glandulosa* is Wells (2000a), which is little changed from Wells (1987). There are a number of features of his treatment that we believe can be improved. Wells' classification relied on induction rather than quantitative analysis. Although he claimed that he had examined a large array of phenetic traits, none of these data were presented in support of his treatment of this or most other species. In addition, he was not a prolific collector and seldom made extensive collections of populations and provided no quantitative comparisons of the range of variability between populations or between subspecific taxa. We have focused in this paper on a quantitative examination of population variation for a large array of phenetic traits, and on populations distributed throughout the range of *A. glandulosa.* Also Wells relied heavily on herbarium material deposited as part of general collections, mostly collected in the spring and thus lacking fruits. As a consequence no mention of fruit characteristics appear in his treatment of subspecific variation in *A. glandulosa.* There are clear examples where this has resulted in substantial errors; e.g., all burl forming *Arctostaphylos* in the Santa Rosa Mountains of Riverside Co., were treated as *A. glandulosa* Eastw. subsp. *adamsii* (Wells 2000a, and annotated specimens at RSA; see also Munz 1958), but as shown by Keeley et al. (1997a) these plants all posses ovoid apiculate single stone fruits, clearly eliminating any close affinity to *A. glandulosa*; these have been described as *A. parryana* Lemmon subsp. *deserticum* Keeley, Boykin & Massihi.

One of the characteristics of *A. glandulosa* that makes this species taxonomically challenging is that many of the subspecies, which typically form spatially defined allopatric populations of apparently true-breeding forms, occasionally merge in populations that contain mixtures of traits. Wells attempted to recognize these as taxonomic entities by naming 'formas.' These formas could dominate a population or occur as multiple morphs within the same population. We have not used this level of treatment because it is not clear that these 'formas' have phylogenetic significance; i.e., an occasional variant such as an eglandular morphotype within an otherwise glandular taxon may have very different origins across the subspecies' distribution. These 'formas' reflect a fundamental difference between Wells' treatment and that proposed here. He was intent on providing a name for every morphotype present in a population. Our approach is to recognize populations of distinct morphotypes that represent nodes of variation with geograph-

FIG. 1. a) *Arctostaphylos glandulosa* platform-like burl from Mt. Tamalpais, Marin Co; b) young plants with developing burl; c) recently burned platform burl from repeated fire cycles with resprouts at the lower right edge (photographs by J. Keeley).

ically defined distributions. Where these subspecies merge and form mixed populations we recognize these populations as potentially important evolutionary stages but have not attempted to provide names for each morphotype in such populations.

The purpose of the present paper is to investigate patterns of phenetic variation at the intra- and inter-population level for *A. glandulosa*. We have collected several thousand specimens in roughly 80 or more populations from throughout the species' range and recorded 52 characters for each specimen. We examine patterns of phenetic variation in the species and how different populations cluster in phenetic space as a first step to generating a taxonomy of the subspecific variation. We begin by examining a taxon, *A. campbellae* Eastw., that has previously been considered a subspecies of *A. glandulosa* but was removed by Wells (2000a). We then examine the extent to which populations can be characterized as glandular versus non-glandular forms, the latter previously being treated as *A. cushingiana* Eastw. Based on this analysis we recognize three phenetic groups distinguished by differences in branchlet indument, and examine other patterns of subdivision within each of these groups. Our focus throughout is to evaluate how previous taxonomic treatments are supported with this data set.

Taxonomic History

Alice Eastwood (1897) named *A. glandulosa* Eastw. from a specimen on Mt. Tamalpais in Marin Co., California. It was recognized by its long glandular hairs on branchlets and rachises and ability to "stump-sprout" from basal burls and was known to be widely distributed throughout California.

A. cushingiana

Later Eastwood (1933) also named a non-glandular pubescent burl-forming *Arctostaphylos* from lower elevations on Mt. Tamalpais, *A. cushingiana* Eastw. However, Adams (1940) recognized that these two stump-sprouting taxa, *A. glandulosa* and *A. cushingiana*, shared a number of important traits (isofacial leaves, mostly foliaceous lower bracts, and depressed oval fruits with separable nutlets), and he subsumed the latter taxon in *A. glandulosa* with the combination, *A. glandulosa* Eastw. var. *cushingiana* Adams ex McMinn (first treated in McMinn 1939).

For a long time the non-glandular but pubescent "*cushingiana*" taxon was thought to be highly restricted in range. Adams (1940) indicated it was only in the counties north of San Francisco Bay, but Munz (1968) extended its distribution further south to Monterey Co., and Hoover (1970) to San Luis Obispo Co. Our studies presented here demonstrate it is also present throughout southern California and northern Baja California.

Throughout the last half of the twentieth century there has been much controversy over how to best treat these glandular and non-glandular burl-forming manzanitas. Wells (1968) did not recognize either *A. cushingiana* or *A. glandulosa* var. *cushingiana*, and considered the non-glandular "*cushingiana*" to be nothing more than an intra-population morph that did not occur in allopatric populations apart from glandular-haired plants. In stark contrast, Hoover (1970) considered it a valid taxon and even treated *A. cushingiana* at the species level, noting it was the dominant resprouting manzanita, and that it occurred in pure (i.e., entirely non-glandular) populations over the eastern half of San Luis Obispo Co. He justified treating *A. cushingiana* at the species level because in his view, where *A. cushingiana* and *A. glandulosa* were sympatric, the degree of hybridization was no greater than between other well established *Arctostaphylos* species. Howell (1970) as well believed *A. cushingiana* should be given species status and considered it to be widespread in Marin Co. and quite distinct from *A. glandulosa*, both of which occurred in pure allopatric populations.

In a later publication Wells (1987) acknowledged that the non-glandular "*cushingiana*" taxon did form pure allopatric populations, but in his inimical contrary style reiterated his conviction that it should not be recognized as anything more than an intra-population morph. He justified this on the basis that these allopatric populations of "*cushingiana*" were "local populations" that had a similar range as the nominate form of *A. glandulosa* and therefore would be inappropriately treated as a subspecies. We note that this rationale is inconsistently applied to other taxa in Wells (2000a). Wells' taxon *A. glandulosa* subsp. *zacaensis* (Eastw.) Wells was described as having a distribution that overlapped and co-occurred with other *A. glandulosa* subspecies throughout central and southern California. Also, Wells' dismissal of "*cushingiana*" because it comprised only "local populations" is never explained; as an aside, he generally used that term in a pejorative sense and applied it to several taxa he chose not to recognize, but others such as *A. gabrielensis* Wells, which comprises a small handful of plants from Mill Creek Summit in the San Gabriel Mountains, he described as "narrowly endemic," and never as a "local population."

A. glandulosa var. *crassifolia*

Jepson (1922) named a new variety from coastal San Diego Co., *A. glandulosa* Eastw. var. *crassifolia* Jepson, recognized only by its coastal distribution and thick elliptic leaves, but

this taxon was not recognized by Eastwood (1934). Later Jepson (1925) transferred this taxon, renaming it *A. tomentosa* (Pursh) Lindley var. *crassifolia* (Jepson) Jepson, and later claimed the original placement in *A. glandulosa* was a calamitous typographical error (Jepson 1939, p. 47). In this later publication he further defined the range of variability for this taxon as tomentose and without long hairs. Adams (1940), however retained *A. glandulosa* var. *crassifolia* and expanded the definition of this taxon to include non-glandular tomentose branchlets with dark green leaves, and occasional individuals with longer hairs. He also expanded the distribution to include Baja California. Wells (1968) elevated it to subspecies *A. glandulosa* Eastw. subsp. *crassifolia* (Jepson) Wells and later (Wells 1987) justified this based on its allopatric and narrow geographic distribution relative to other morphological types. Wiggins (1980) made an important observation when he noted that the fruits were much wider than tall (consistent with our results presented below) and indicated this taxon was present in northern Baja California. Later Wells (1987) expanded the definition of this taxon to include populations in which 50% of the individuals had long villous hairs, and he gave the range as from Oceanside in San Diego Co. to Cabo Colonett in Baja California. He also considered the range of this taxon to be restricted to coastal outcrops of Eocene age siliceous sandstone. Knight (1981) expanded the distribution of this taxon to include other substrates and further inland (> 10 km from the coast, e.g., Mt. Whitney near Escondido), thus including populations that were substantively different from the type in that they included ones with glandular hairs not unlike the nominate form. As a consequence he concluded that the taxon *A. glandulosa* subsp. *crassifolia* had no validity and was the product of hybridization of *A. glandulosa* with other manzanitas in the area; however presently there are no other *Arctostaphylos* species this close to the coast in San Diego Co. Knight (1981) also reported non-burl forming individuals in the Encinitas population of this taxon, but field observations (Keeley unpublished data) revealed that all such individuals were from layered branches that had rooted and in many instances still maintained connections with burl forming plants.

A. campbellae

Eastwood (1933) named *A. campbellae* Eastw. as a non-glandular tomentose species, separated from *A. cushingiana* by its branchlets with long spreading hairs, present on Mt. Hamilton, Santa Clara Co. She made no mention of it being a sprouting species, but Adams (1940) noted the enlarged root crown as one of the reasons for subsuming it as *A. glandulosa* Eastw. var. *campbellae* (Eastw.) Adams. He also extended the range to include the lower foothills to the east of Mt. Hamiliton in San Antonio Valley, Santa Clara Co. McMinn (1939), apparently lumping it with plants we now recognize as *A. glandulosa* subsp. *mollis* (see below), considered *A. glandulosa* subsp. *campbellae* to be very widely distributed, including the Santa Ynez and San Gabriel Mountains in southern California Transverse Ranges. Hoover (1970) concurred that this variety occurred outside of Santa Clara Co. and noted locations in San Luis Obispo Co. Wells (1987), however, disputed the relationship between *A. campbellae* and *A. glandulosa* and contended that the type population on Mt. Hamilton was a hybrid swarm between *A. crustacea* Eastw. (which he treated as *A. tomentosa* (Pursh) Lindley subsp. *crustacea* (Eastw.) Wells) and *A. glauca* Lindley, and he did not consider the *A. campbellae* taxon to have a close relationship to *A. glandulosa.*

A. zacaensis

In 1933 Eastwood named *A. zacaensis* Eastw., a burl-forming species with pale leaves and glandular hairs from the slopes surrounding Zaca Lake in Santa Barbara Co. Later, Eastwood (1934) suggested this taxon occurred south in San Diego Co. and McMinn (1939) concurred with this range, but followed Adams' (1940) treatment of these plants as *A. glandulosa* Eastw. var. *zacaensis* (Eastw.) Adams. Subsequently, Wells (1968) changed this taxon to *A. glandulosa* Eastw. subsp. *zacaensis* (Eastw.) Wells and considered it the appropriate name for all *A. glandulosa* lacking eglandular setose hairs, but with foliaceous bracts and any degree of glaucous foliage (Wells 1987). He believed this subspecies did not occur north of Santa Cruz Co. and that it displaced the nominate subspecies south of San Francisco. Additionally, it could occur sympatrically with other subspecies such as *A. glandulosa* subsp. *crassifolia* (Wells 1987) and *A. glandulosa* subsp. *adamsii* (annotation labels on *Munz & Balls 17941*, RSA).

A. howellii

Also in 1933, Eastwood named *A. howellii* Eastw., a Monterey Co. pubescent taxon much like *A. cushingiana* but with glandular rachises. McMinn (1939) added that it had glandular fruits. This taxon was recombined as *A. glandulosa* Eastw. var. *howellii* Adams ex McMinn (McMinn 1939) and later *A. glandulosa* Eastw. subsp. *howellii* (Wells 1968). Hoover (1970) suggested this taxon was "an apparent intergrade" between *A. glandulosa* and *A. cushingiana* and did not formally recognize it. In later treatments, Wells (1987, 2000a) also did not formally recognize this taxon and considered it to be a morphological form of *A. glandulosa* subsp. *zacaensis.*

A. glandulosa var. *mollis* and *A. glandulosa* subsp. *glaucomollis*

Adams (1940) named a non-glandular puberulent form with long setose hairs and foliaceous bracts *A. glandulosa* Eastw. var. *mollis* Adams, based on specimens from La Cumbre Peak in the Santa Ynez Range of Santa Barbara Co. Munz (1959) expanded the circumscription of this taxon to include deltoid-shaped upper bracts and expanded the distribution northward to San Luis Obispo Co. and southward to Riverside Co. Wells (1968) changed the subspecific classification with the recombination, *A. glandulosa* Eastw. subsp. *mollis* (Adams) Wells. Later he named *A. glandulosa* Eastw. subsp. *glaucomollis* Wells (1987), another non-glandular form with setose hairs separated from *A. glandulosa* subsp. *mollis* by having reduced upper bracts. Wells considered the more foliaceous-bracted subsp. *mollis* to be restricted to the western end of the Transverse Ranges and the reduced-bracted subsp. *glaucomollis* to be restricted to the central and eastern Transverse Ranges.

A. glandulosa var. *adamsii*

Another non-glandular pubescent form from interior San Diego and Riverside counties was named by Munz (1958) as *A. glandulosa* Eastw. var. *adamsii* Munz. It was recognized by the intensely glaucous leaves and highly reduced deltoid bracts and lack of glandular hairs. Subsequently, Munz (1974) treated this as a subspecies. Wells (1987) expanded the definition of this taxon to include densely glandular forms as well as the non-glandular tomentose forms in the type population, and commented that this was the most common form, a detail that, in his words, Munz had "either overlooked or ignored." Later Wells (2000a) further expanded the definition, not only of this taxon, but of the species *A. glandulosa*, by including populations with glabrous branchlets, which justified his subsuming the newly described *A. incognita* Keeley, Massihi and Delgadillo (1997b) into *A. glandulosa* subsp. *adamsii*.

A. gabrielensis

On a brief field trip led by the senior author (JEK), Phil Wells collected a few specimens from a roadside population at Mill Creek Summit in the San Gabriel Mountains and named *A. gabrielensis* Wells (Wells 1992), a taxon he suggested had similarities to four other species of *Arctostaphylos*, but *A. glandulosa* was not one of them. However, later Wells (2000a) reversed this opinion and concluded that *A. gabrielensis* was actually a hybrid between *A. glandulosa* and *A. parryana* Lemmon. Wells considered the combination of a resprouting population with single stone fruits resulting from cohesion of endocarp segments to represent a unique combination and worthy of recognition at the species level. However, his lack of population-level study of the Mill Creek Summit population misled him because the solid stones of fused endocarp drupelets present in the type specimen (Wells and Keeley 31086 CAS), as will be shown below, are an uncommon trait in this population. Also, the phenetic analysis presented here will show that *A. gabrielensis* falls well within the range of variation for *A. glandulosa* in the interior portions of the San Gabriel Mountain Range.

Other Taxa

Adams (1940) named several other varieties of *A. glandulosa*. One of these, *A. glandulosa* var. *australis* Adams from southwestern San Diego Co., was based mostly on leaf shape characteristics. Munz (1959), who followed most of Adams' treatment for *Arctostaphylos*, did not recognize this variety, and Wells (1987) considered this a form of *A. glandulosa* subsp. *zacaensis*.

Other taxa associated with *A. glandulosa* at one time or another include the following. *Arctostaphylos glandulosa* var. *vestita* (Eastw.) Jepson (1922) has been considered to be *A. tomentosa* (Pursh) Lindley in all subsequent treatments because the bifacial leaves separate it from the isofacial leaves of *A. glandulosa*. Also, *A. glandulosa* var. *virgata* (Eastw.) Jepson (1922) was named from Mt Tamalpais, but subsequent authors have noted the lack of a basal burl and treated this taxon as *A. virgata* Eastw. Wells (2000a) considered *A. virgata* to be substantially different from *A. glandulosa* in a number of leaf and bract characteristics and placed in a separate subsection.

Methods

Several thousand herbarium specimens of *A. glandulosa* and related taxa were collected by the lead author (JEK) and students over a period of several years and deposited at RSA. It was not logistically feasible to systematically collect equally from all parts of the vast range of this species. We made inferences about where collections were likely to be most informative. The information that most influenced our collecting sites were: (i) prior knowledge of variation not clearly accounted for by past taxonomic treatments, (ii) areas occupied by previously described subspecies, and (iii) regions where there had not been much prior collecting. Since 5 of the 6 recognized subspecies in Hickman (1993) are southern California endemics, collecting was concentrated in the southern half of the state. Because Baja California had been poorly studied, further concentration was given to that region as well. Collections were restricted to late summer

TABLE 1. MORPHOLOGICAL TRAITS SCORED OR CALCULATED FOR *A. GLANDULOSA* SPECIMENS. Not all of these traits are informative about intraspecific variation in this species but have been included as part of a larger study of trait variation in the genus.

Burl	no burl = 1, burl = 5
Leaves	
Blade length	measured (mm)
Blade width	measured (mm)
Length/width	calculated ratio
Petiole length (mm)	measured (mm)
Blade basal angle	measured (°)
Blade apical angle	measured (°)
Stomata (adaxial surface)	density
Stomata (abaxial surface)	density
Stomatal ratio	adaxial density/abaxial density
Color	1 = yellow, 3 = yellow-green, 5 =green
Luster	1 = glaucous, 3 = intermediate, 5 = glossy
Scabrous	1 = smooth, 3 = intermediate, 5 = scabrous
Indument pubescence	1 = glabrous, 2–3 = short pubescences, 4–5 = long hairs
Scored for branchlets, old leaves, new leaves, rachises, pedicels, and fruits separately	
Indument glandularity	1 = glabrous, 2–3 = viscid glands, 4–5 = long glandular hairs
Scored for branchlets, old leaves, new leaves, rachises, pedicels, and fruits separately	
Nascent inflorescence	
Orientation	1 = descending, 3 = ascending, 5 = erect
Bract spacing	1 = overlap to 5 = well spaced
Bract keel	1 = no, 3 = moderate, 5 = deeply keeled
Bract shape	1 = lanceolate, 3 = deltoid-acuminate, 5 = ovate
Bract tip marcescent	1 = no, 5 = yes
Bract reflexed	1 = no, 5 = yes
Bract length (lower)	measured (mm)
Bract length (upper)	measured (mm)
# of rachis branches	
Fruiting inflorescence	
Rachis length	measured (mm)
Pedicel length	measured (mm)
Sepal shape	1 = obtuse, 5 = acuminate
Sepals reflexed	1 = no, 5 = yes
Fruits	
Color	1 = tan, 2 = orange, 3 = red, 4 = brown, 5 = purple
Height	measured (mm)
Width	measured (mm)
Width/height	calculated ratio
Mass of entire fruit	measured (g)
Mesocarp	1 = mealy, 3 = leathery, 5 = papery
Mass of endocarp	measured (g)
# of endocarp segments	measured (g)
Endocarp height	measured (mm)
Endocarp width	measured (mm)
Endocarp width/height	calculated ratio
Endocarp apiculate	1 = no, 5 = yes
Endocarp ridges	1 = no, 5 = yes
Endocarp sculpturing	1 = no, 5 = yes

or fall in order to increase the chances of obtaining specimens with both mature fruits and nascent inflorescences, both of which are key characters in *Arctostaphylos* taxonomy and far more critical in most cases than flowers. When possible, population samples of 15–30 or more individuals were collected. Dried specimens that possessed both fruits and nascents were scored for 48 (23 vegetative and 25 reproductive) traits and 4 other traits were calculated (Table 1). Stomatal density was determined from clear nail polish impressions that were peeled off leaves, mounted on glass slides and viewed at 40× with a compound microscope.

Eighty populations were sampled, but those with fewer than 5 individuals were eliminated

from further analysis, leaving a total of 1342 plants distributed across 69 populations. The average score for each trait was calculated for each population.

Our initial analysis of all *A. glandulosa* populations included all characters in a multivariate analysis using PC-ORD (McCune and Mefford 1999). Nonmetric multidimensional scaling (NMS), Principal Components Analysis and Reciprocal Averaging were used to examine relationships among the populations. Character scores were relativized to range between 0 and 1.0 to prevent weighting of characters.

For our initial analysis of the relationship of *A. campbellae* to *A. glandulosa*, and for other intraspecific analysis we used cluster analysis. Using the population by trait data matrix, all variables were standardized as z-scores by subtracting the variable sample mean from each value and then dividing the difference by the sample standard deviation. This data matrix was used in the Hierarchical Cluster procedure that calculated normalized Euclidean distance (root mean squared distances) and expressed the results as dendrograms with distance metrics. Traits selected were those generally considered important in separating infra-specific taxa in *A. glandulosa*. In order to avoid overly weighting certain types of characters, traits that exhibited high colinearity, as shown with least squares regression, were avoided. Traits were removed if they did not greatly contribute to the initial cluster pattern. Thus, generally most analyses included only 1 or 2 traits from the following trait classes: leaf color and shape, indument, inflorescence bracts, and fruits. The primary criterion for whether or not a cluster was relevant to our study of subspecific variation patterns was if clustered populations shared similar geographical and ecological situations. Where group comparisons were made, this was with Kruskal-Wallis test using population mean values. All analyses other than the multivariate analyses described in the previous paragraph, utilized the SYSTAT 11 statistics software (www.systat.com).

Results

Evaluating the Inclusion of *A. campbellae*

In order to make a decision as to whether or not the taxon originally described as *A. campbellae* should be included in this treatment of *A. glandulosa* we made the following comparison. The type population on Mt. Hamilton (Santa Clara Co.), and a couple similar populations from San Antonio Valley (Santa Clara Co.) just to the east of Mt. Hamilton, all treated by Adams (1940) as *A. glandulosa* var. *campbellae*, were compared with three species previous authors suggested had close affinities: *A. crustacea, A. glandulosa*, and *A. glauca*. The *A. glandulosa* population was from the type locality (La Cumbre Peak) of *A. glandulosa* subsp. *mollis*, chosen for comparison because it exhibits several features in common with *A. campbellae*, including branches that are non-glandular and pubescent with long setose hairs. *Arctostaphylos crustacea* is also non-glandular with long setose hairs but is distinguished from *A. glandulosa* in having bifacial leaves in which the upper leaf surface is astomatous, in contrast to the isofacial leaves of *A. glandulosa* that are considered to have similar stomatal densities on both surfaces (Howell 1945). *Arctostaphylos glauca* was included because Wells (2000a) considered *A. campbellae* a hybrid between *A. crustacea* and *A. glauca.*

In light of these differences, one of the first characters to assess was stomatal distribution (Table 2). As expected, our population of *A. crustacea* lacked stomata on the upper leaf surface, and our *A. glandulosa* population had many stomata on the upper leaf surface, however, surprisingly this population of *A. glandulosa* subsp *mollis* had only 37% as many stomata on the upper surface as the lower surface. The *A. campbellae* populations were between these two extremes: 6, 15, and 23% for the Mt. Hamilton, southern San Antonio and northern San Antonio populations, respectively. *Arctostaphylos glauca* stomata were evenly distributed on both surfaces and the density was greater than on any of the other taxa.

The cluster analysis was based on 10 vegetative traits and 12 reproductive traits (Fig. 2). It indicated that the *A. campbellae* populations were morphologically closer to *A. crustacea*, but both of these taxa were much more closely aligned with *A. glandulosa* than with *A. glauca.* The *A. campbellae* populations may represent a subspecific variant of *A. crustacea*, recognized by the presence of some stomata on the upper leaf surface, the consistent presence of tomentum on the lower surface, and the rounded to obtuse leaf bases. Regardless, we have not considered *A. campbellae* populations further in this analysis of *A. glandulosa* subspecific variation.

A. glandulosa Population Patterns: Glandular vs Non-Glandular

Because of the long standing difference of opinion on the reality of a non-glandular pubescent "*cushingiana*" taxon distinct from the glandular taxon in *A. glandulosa*, we began by asking whether or not glandular plants were separable in trait space from non-glandular plants. We compared several ordination methods and all produced similar patterns, but only the nonmetric multidimensional scaling (NMS) results are presented (Fig. 3). In this analysis we utilized the entire data matrix of 52 characters

TABLE 2. STOMATAL DISTRIBUTION ON UPPER AND LOWER LEAF SURFACES IN *ARCTOSTAPHYLOS GLANDULOSA* AND ASSOCIATED SPECIES' POPULATIONS.

	Leaf stomata	
	Density on lower surface (# / mm²)	Upper/lower surface ratio
Taxon population(s)	X̄ (range)	X̄ (range)
A. crustacea	21.8 (14.6–28.3)	< 0. 01
A. campbellae		
Mt. Hamilton	17.9 (13.3–24.8)	0.06 (<0.01–0.26)
Southern San Antonio Valley	21.6 (16.4–33.2)	0.15 (<0.01–0.46)
Northern San Antonio Valley	21.2 (19.6–29.2)	0.23 (0.08–0.35)
A. glandulosa		
subsp. *mollis* (Munz) Wells	16.8 (10.6–24.3)	0.37 (0.20–0.54)
Group A	27.9 (14.9–32.4)	0.74 (0.52–0.93)
Group B	27.0 (15.6–32.2)	0.77 (0.41–1.02)
Group C	27.8 (16.8–31.8)	0.71 (0.37–0.71)
A. glauca	31.5 (19.6–41.9)	1.0 (0.83–1.7)

and all 69 populations, although five outlier populations were removed from the final analysis. This analysis is presented in Figure 3 with different symbols for three categories: a) glandular (black triangles), b) non-glandular short tomentose (gray squares) and c) non-glandular short tomentose plus long setose hairs (white diamonds). In this analysis most populations designated as glandular sorted out in trait space separate from non-glandular plants. Glandular populations had a population mean score for glandular branchlets (on a scale from 1–5) of 4–5 with the cutoff being 2.9, comprising 26 populations and represented as Group A in subsequent analyses (Table 3). Non-glandular plants were the only or dominant form in over half of the populations, and these made up Groups B and C, dependent on whether or not they possessed long setose hairs (Table 3). Of these, the vast majority were homogenous with respect to lack of glandularity; out of the 43 populations comprising Groups B and C, all but six had a coefficient of variation (CV) for the glandularity index that was 0–50%, indicating relatively limited varia-

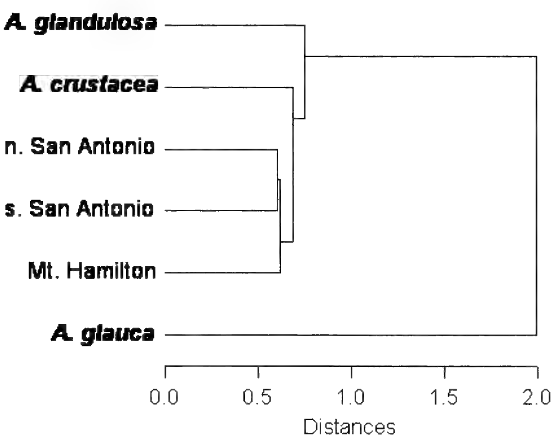

FIG. 2. Hierarchical cluster analysis for of *A. campbellae, A. crustacea, A. glandulosa and A. glauca*. The *A. campbellae* populations were from the type locality (Mt. Hamilton, Santa Clara Co.) and southern and northern ends of the valley east of Mt. Hamilton (n. or s. San Antonio), n = 19, 15 and 8 respectively; *A. crustacea* from San Benito Co., n = 11; *A. glandulosa* subsp. *mollis* from the type population on La Cumbre Peak, Santa Barbara Co., n = 13; *A. glauca* from Los Angeles Co., n = 35. Cluster analysis was based on population means for the following leaf traits, length, width/length ratio, basal angle, luster, scabrous, abaxial stomatal density, stomata ad-/abaxial ratio; other vegetative traits, burl, branchlet pubescence; reproductive traits, bract spacing, bract shape, bract reflex, lower bract length, middle bract length, rachis length, fruit color, fruit height, mesocarp, number of stones, apiculate, and fruit width/height ratio.

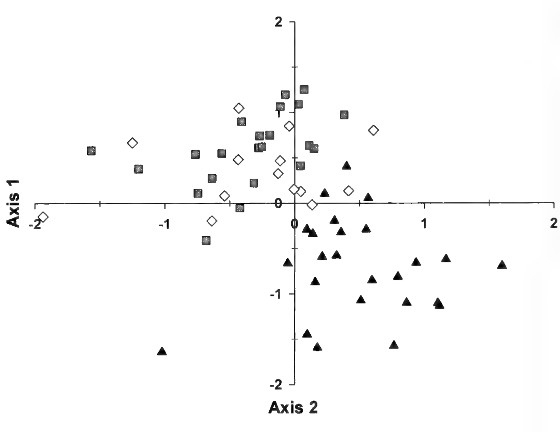

FIG. 3. Nonmetric multidimensional scaling ordination for all characters and all 69 populations, although five outlier populations were removed from the final analysis; populations were classified as glandular (black triangles), non-glandular short tomentose (gray squares) or non-glandular short tomentose plus long setose hairs (white diamonds) as described in Table 3.

tion. Several populations had a CV between 70–78% resulting from a mixture of some glandular plants in an otherwise non-glandular population.

Comparison Between Glandular and Non-Glandular Groups

Subsequent analyses were based on analyzing patterns of variation both between (this section) and within (next section) glandular and non-glandular groups (Table 3). The ordination analysis on all traits clearly separated the glandular from the non-glandular populations, however, within the non-glandular forms the populations with long setose hairs overlapped in trait space with populations lacking such hairs (Fig. 3). We made the decision to weight this trait more heavily than others because setose hair populations occurred in geographically restricted areas with limited overlap with other forms, and because this trait has been weighted heavily in previous taxonomic treatments. Thus, for subsequent analysis we retained the subdivision of non-glandular populations into those without (Group B) and those with setose hairs (Groups C).

Groups were not significantly different in mean latitude of distribution (using the Kruskal-Wallis test), but Group A populations tended to occur at lower elevations and closer to the coast than Group C ($P < 0.01$). In addition to the branchlet glandularity trait on which Group A was based, there were parallel differences in glandularity of other structures; Group A had significantly ($P < 0.001$) greater glandularity for leaves, rachises, pedicels and fruits than Groups B and C. There were five other traits for which Group A exhibited highly significant ($P < 0.001$) differences from both Groups B and C; Group A leaves were much more scabrous, and they had longer rachises, and narrower, less keeled, and less marcescent bracts. Lower bracts in Group A were significantly ($P < 0.001$) longer than in Group B, but Group C was not significantly different from the other two groups in this trait. Group B sepals were significantly more reflexed than Group A and the number of endocarp segments were significantly fewer than in either Groups A or C ($P < 0.05$).

Comparisons Within the Glandular Group A

Cluster analysis of Group A with several different selections of leaf, inflorescence and fruit characters (not shown) failed to uncover any clusters tied to a particular geographical region or ecological habitat. This glandular group did, however, have two variants worth recognizing, each based on a single divergent trait. One was a unique population (A2 Punta Banda lower, Table 3) that lacked basal burls, and observations in a recently burned area indicated it also failed to resprout. In other vegetative and reproductive traits it was not separable from nearby resprouting glandular populations. Another recognizable variation was a number of populations that had leaves covered with a heavy glaucous bloom. This was explored in greater detail because Wells (1987; 2000a) used this trait to separate non-glaucous northern California *A. glandulosa* Eastw. subsp. *glandulosa* from glaucous central and southern California *A. glandulosa* Eastw. subsp. *zacaensis* (Eastw.) Wells. Cluster analysis on just leaf luster, color and shape revealed two populations with very intensely glaucous leaves separated clearly from all other populations in this group (populations A3 from Baja California and A16 from San Diego Co., top of Fig. 4). These heavily glaucous plants also tended towards long foliaceous inflorescence bracts. Relative to these two populations, other glandular populations grouped together forming sub-clusters reflecting differing degrees of glaucousness that ranged from somewhat glaucous (A14 and A18, from interior ranges in San Diego and Riverside counties) to largely (A12 and A13) or entirely (A6) non-glaucous populations from more coastal mountains in San Diego Co.

Comparisons Within the Non-Glandular Group B

Cluster analysis of the non-glandular plants in Group B is shown in Fig. 5 based on leaf characters of length/width ratio, color, luster, and pubescence on old leaf blades, nascent inflorescence orientation, sepals reflexed, and fruit characters including mass, width/height ratio and pubescence on the outside pericarp. Population B1 (top of Fig. 5), near the village of La Candelaria in Baja California, exhibited the greatest separation distance and was unique in that most of the plants in the population had erect nascent inflorescences, in contrast to the pendent orientation of all other populations of *A. glandulosa.*

Two other clusters of populations are worth noting because within each cluster are populations in close geographical proximity, plus these clusters match previously described taxa. One of these (B8, B9 and B10, bottom of Fig. 5) comprises populations located along the immediate coast in San Diego Co., and historically has been recognized as *A. glandulosa* Eastw. subsp. *crassifolia* (Jeps.) Wells. This cluster was highly dependent on the inclusion of fruit shape and mass. The average fruit width/height ratio for all populations in this study was 1.3, whereas the three San Diego coastal populations (B8, B9 and B10) ranged from 1.6–1.9, indicating much more flattened fruits than typical for the species. In addition these populations had rather small fruits,

TABLE 3. *ARCTOSTAPHYLOS GLANDULOSA* POPULATIONS USED IN NONMETRIC MULTIDIMENSIONAL SCALING AND HIERARCHICAL CLUSTER ANALYSIS, DIVIDED INTO GLANDULAR AND NON-GLANDULAR POPULATIONS. The latter were further subdivided into those with short canescent or tomentose branchlets and those that also had longer setose hairs. Populations with fewer than 5 specimens were not included, resulting in 1342 individuals distributed between 69 populations. Group A, glandular haired populations typically had branchlet glandularity scored 4–5 (on a scale from 1–5) with the minimum population mean of 2.9. Group B populations lacked long setose hairs unlike Group C populations, which were dominated by plants with long hairs.

	Population	County	Latitude	Elevation (m)	Distance (km)	*N*
Group A: Glandular hairs						
A1	Punta Banda upper	n. Baja	31°40′	650	3	27
A2	Punta Banda lower	"	31°41′	630	2	18
A3	Cerro Bolo Peak	"	32°19′	1220	30	43
A4	Tecate	San Diego	32°29′	760	44	8
A5	Otay Mtn	"	32°37′	970	28	35
A6	San Miguel Mtn	"	32°43′	310	25	15
A7	Los Pinos	"	32°45′	1270	57	18
A8	Japutal Valley Rd	"	32°49′	1040	53	17
A9	Guatay	"	32°51′	1120	67	5
A10	Escondido	"	33°08′	450	17	35
A11	Carlsbad	"	33°09′	90	5	31
A12	Merriam Mtns	"	33°13′	400	20	36
A13	San Marcos	"	33°13′	445	20	37
A14	Palomar Mtn (east)	"	33°16′	1085	57	18
A15	Palomar Mtn (west)	"	33°20′	1470	49	22
A16	Palomar Mtn (north)	"	33°20′	1470	63	39
A17	Palomar Peak	"	33°22′	1870	61	15
A18	Rancho California	Riverside	33°30′	830	28	8
A19	Red Mtn	"	33°37′	1100	55	10
A20	Blue Jay Camp	Orange	33°45′	1575	70	41
A21	San Jacinto	Riverside	33°46′	1570	70	41
A22	Refugio Pass	Santa Barbara	34°32′	935	12	56
A23	Figueroa Mtn	"	34°45′	1155	46	13
A24	Chews Ridge	Monterey	36°18′	1485	19	15
A25	Mt. Tamalpais	Marin	37°55′	525	4	11
A26	West Point Inn	"	37°55′	500	5	6
Group B: No glandular hairs, indument only tomentose or short canescent						
B1	La Candelaria	n. Baja	31°53′	580	24	42
B2	Tres Aguajes	"	31°55′	490	16	15
B3	Sierra Juarez	"	31°57′	1390	59	17
B4	Cerro Bolo (base)	"	32°19′	700	31	19
B5	El Condor	"	32°29′	1200	125	18
B6	Potrero Peak	San Diego	32°38′	870	50	6
B7	Cottonwood	"	32°47′	1350	78	24
B8	Del Mar	"	32°57′	115	1	6
B9	San Dieguito	"	33°00′	90	4	7
B10	Encinitas	"	33°03′	95	3	21
B11	Glendora Ridge	Los Angeles	34°13′	1410	80	19
B12	Shortcut	"	34°16′	1400	53	10
B13	Windy Gap	"	34°17′	1545	59	11
B14	Chilao	"	34°19′	1600	59	13
B15	Mt Gleason Peak	"	34°22′	1790	52	30
B16	Mt Gleason (base)	"	34°23′	1520	57	11
B17	Mill Creek Summit	"	34°23′	1470	60	20
B18	Pacifico	"	34°23′	1735	61	28
B19	Mt Gleason (midway)	"	34°23′	1670	55	28
B20	Rose Valley	Ventura	34°32′	1150	32	11
B21	Reyes Peak	"	34°38′	2030	37	10
B22	Pine Mtn	"	34°39′	1750	37	21
B23	Bates Canyon	Santa Barbara	34°46′	1375	89	15
B24	Sierra Madre Ridge	"	34°55′	1570	92	47
B25	Black Mtn	San Luis Obispo	35°23′	1080	40	26
B26	Mill Valley	Marin	37°55′	130	7	15
B27	Drakes Hwy	"	38°10′	120	5	10
B28	Mt. St Helena	Sonoma	38°40′	1100	49	16

TABLE 3. CONTINUED.

	Population	County	Latitude	Elevation (m)	Distance (km)	*N*
Group C: No glandular hairs but longer setose hairs						
C1	Enrendira	n. Baja	31°13′	60	4	15
C2	Kitchen Creek	San Diego	32°48′	1460	71	30
C3	Laguna Mtns	"	32°57′	1615	75	31
C4	Angeles Oaks	San Bernardino	34°08′	1660	104	10
C5	Santa Ana River	"	34°12′	1700	110	22
C6	Seven Oaks	"	34°13′	1920	113	18
C7	Switzers	Los Angeles	34°16′	1070	46	6
C8	Lytle Creek	San Bernardino	34°17′	1595	80	20
C9	Lake Arrowhead	"	34°18′	1580	103	12
C10	Crystal Lake	Los Angeles	34°19′	1720	70	13
C11	La Cumbre Peak	Santa Barbara	34°29′	1185	13	13
C12	Camino Cielo East	"	34°30′	1110	15	7
C13	Liebre Mtns	Los Angeles	34°43′	1670	82	23
C14	Zaca Peak	Santa Barbara	34°47′	1125	51	7
C15	La Cuesta	San Luis Obispo	35°21′	600	22	7

with fruit mass ranging from 100–161 mg whereas the mean for all populations was 251 mg.

A second cluster (B3, B4, B5, and B7, near the top of Fig. 5) included populations, from southeastern San Diego Co. and adjacent Baja California. This cluster was sensitive to the inclusion of leaf and bract traits and these plants were characterized by intensely glaucous leaves and highly reduced bracts, matching closely the original description of *A. glandulosa* Eastw. var. *adamsii* Munz.

Further analysis of Group B was prompted by the fact that one of the populations (B17 Mill Creek Summit, Table 3) was the type locality for *A. gabrielensis* Wells. Cluster analysis was done on the Group B data after removing those populations discussed above, using the characters considered by Wells (1992) as critical in distinguishing *A. gabrielensis* as a new species: leaf color, luster, glabrousness, bract length and number of endocarp segments. In this cluster analysis (Fig. 6) the *A. gabrielensis* population (B17) was clearly embedded within a cluster of other *A. glandulosa* populations (B11, B13, B14, B15, B16, B18, and B19), all of which are located in the interior San Gabriel Mountains (Table 3). A phenetically similar disjunct population (B24, Fig. 6) occurs in the Sierra Madre Mountains of Santa Barbara Co. Morphologically these populations are all recognizable by their glabrous and highly lustrous leaves as well as their reduced bracts and a tendency for endocarp segments to remain consolidated in 1 or 2 segments.

Because Wells (2000a) speculated that *A. gabrielensis* was of hybrid origin between *A. glandulosa* and *A. parryana* Lemmon we did a cluster analysis using 283 specimens from an earlier study of burl-forming populations of *A. parryana* (Keeley et al. 1997a). Using the same traits listed above we found *A. parryana* was close to the cluster of populations in the interior San Gabriel Mountains (cluster diagram not shown), reflecting the close phenetic similarity between these taxa. Fruit characteristics provide the clearest differences between *A. parryana* from *A. glandulosa* (Table 4). The former species has large solid round endocarp stones with apiculate tips, whereas typical *A. glandulosa* fruits are flattened and break apart into multiple segments. The interior San Gabriel Mountains populations of *A. glandulosa*, including the Mill Creek type population for *A. gabrielensis*, showed a tendency towards certain aspects of *A. parryana* fruits, including the larger size and a tendency for producing some fruits with solid apiculate stones.

Comparisons Within the Non-Glandular Group C

Non-glandular plants with long setose or hispid hairs represented collections that Wells (1987, 2000a) had subdivided into two subspecies, *A. glandulosa* Eastw. subsp. *mollis* (Adams) Wells and *A. glandulosa* Eastw. subsp. *glaucomollis* Wells. The basis for this separation was the contention that the former had foliaceous bracts and was restricted to the western end of the Transverse Ranges, and the latter had reduced bracts and was restricted to the central and eastern end of the Transverse Ranges. Our initial group comparison did show that both bracts were present in Group C, reflected in our comparison among groups; Group A had significantly longer bracts than Group B, but Group C was not significantly different from either A or B. However, we found no geographical basis for the distribution of bract length in Group C that would support Well's treatment. Cluster analysis using bract length alone (not shown) failed to reveal any geographic clustering, due to the fact that long foliaceous bracts were present in populations throughout the Transverse Ranges.

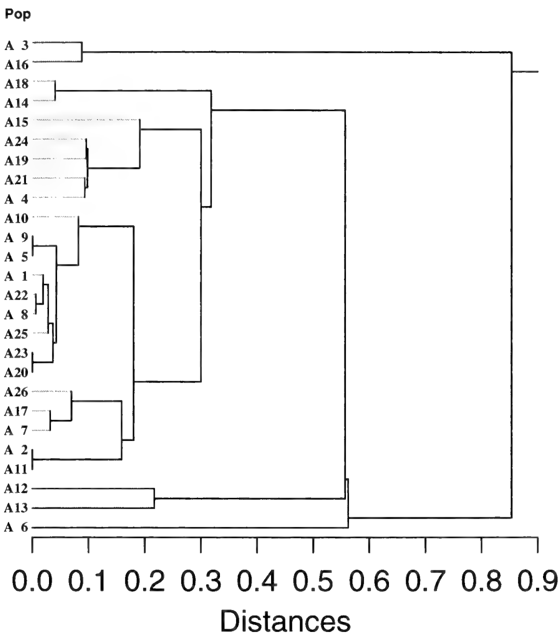

FIG. 4. Cluster analysis for Group **A** glandular plants for leaf traits, luster, color and length/width ratio. See Table 1 for trait description and Table 3 for population information. Note that populations within a group are arranged by latitude and so the numerical order of populations reflects their proximity to one another.

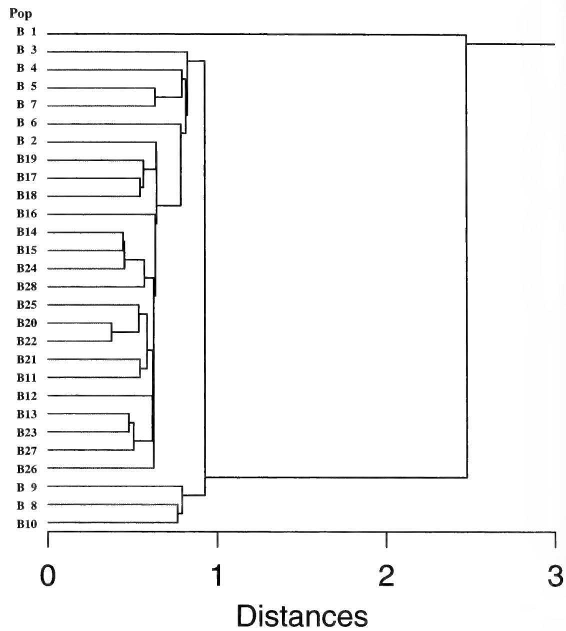

FIG. 5. Cluster analysis for Group **B** non-glandular plants with tomentose branchlets. Traits included leaf characters of length/width ratio, color, luster, and pubescence on old leaf blades, nascent inflorescence orientation, sepals reflexed, and fruit characters including width/height ratio, pubescence on the outside pericarp, type of mesocarp, and number of endocarp segments. See Table 1 for trait description and Table 3 for population information.

In the study of *A. campbellae* populations reported above it was demonstrated that the type population for *A. glandulosa* subsp. *mollis* from La Cumbre Peak in Santa Barbara Co. had a tendency towards bifacial leaves. This was evident in greatly reduced stomatal density, and greater luster, on the upper leaf surface. Comparison of stomatal patterns for this population with other averages for the three *A. glandulosa* groups (Table 2) revealed the surprising result that very few *A. glandulosa* populations had equal densities of stomata on both leaf surfaces as suggested by Howell (1945). On average Groups A, B and C all had about 25% fewer stomata on the upper leaf surface, although there was a great deal of variation within each group. The type population for *A. glandulosa* subsp. *mollis* had the lowest ratio for all *A. glandulosa* populations, but the ranges shown in Table 2 reveal that there are populations in the other groups that come close in having substantially fewer stomata on the upper leaf surface. Regression analysis showed that the ratio of upper/lower leaf surface stomata was correlated with environmental patterns; e.g., it was negatively related to latitude and positively tied to elevation and distance from the coast ($P < 0.05$).

The cluster analysis of Group C was repeated including stomatal characters along with other leaf and bract characters (Fig. 7). This analysis showed that the type population for *A. glandulosa* subsp. *mollis* (C11, top of Fig. 7) was somewhat distinct from the other Group C populations. The next closest population (C13) was also from the western Transverse Ranges and in both cases these were populations with relatively low stomatal ratios. Other populations (C12, C14, and C15) from the western end of the Transverse Ranges had phenetic patterns not too dissimilar to populations in the eastern end of range. Thus, other than a tendency for reduced stomatal density on the upper leaf surface in some populations from the western end of the Transverse Ranges, this analysis does not support any strong geographical association with leaf or bract traits.

Finally, several of the Group C populations were mixtures of plants with and without these long hairs. These mixed populations included a couple in the Transverse Ranges — Seven Oaks (C6) in the San Bernardino Mountains and Crystal Lake (C10) in the San Gabriel Mountains — as well as a few populations outside of the Transverse Ranges, including Erendira (C1) in northern Baja California, Kitchen Creek (C2) and Laguna Mountains (C4) in San Diego Co.

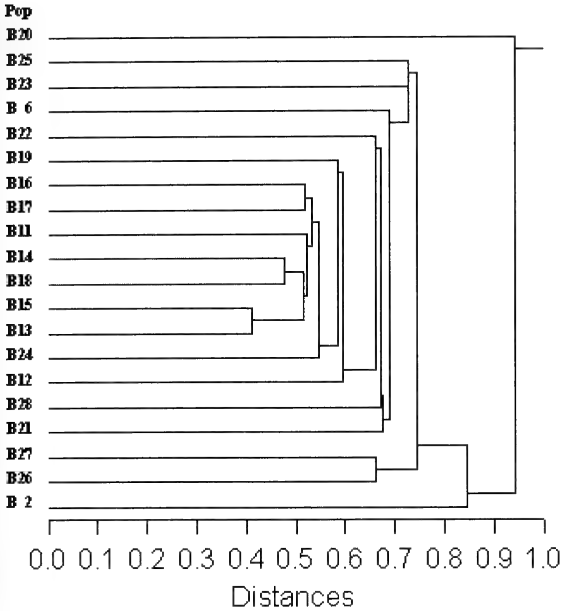

FIG. 6. Cluster analysis for Group **B** non-glandular plants with tomentose branchlets but with the three clusters represented in Figure 5 by populations 1, and 3, 4, 5, 7, and 8, 9, 10 removed. Analysis of remaining populations in Group **B** were with leaf characters of length/width ratio, color, luster, lower bract length, sepals reflexed, and fruit characters including width/height ratio, type of mesocarp, and number of endocarp segments. See Table 1 for trait description and Table 3 for populations described by the case numbers.

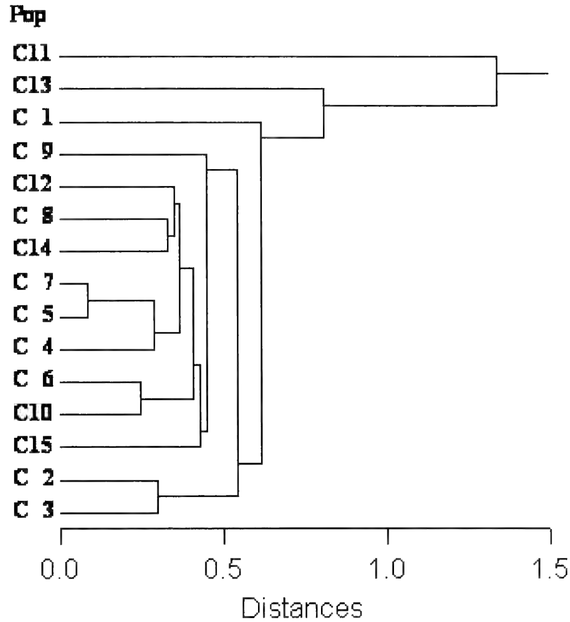

FIG. 7. Cluster analysis for Group **C** non-glandular plants with setose hairs for lower and upper bract length. See Table 1 for trait description and Table 3 for populations described by the case numbers.

TAXONOMIC TREATMENT

We hypothesize that glandular and non-glandular tomentose populations are two lineages that occur throughout the coastal ranges of California and northern Baja California. Some previous taxonomic treatments have given these two taxa status as distinct species, *A. glandulosa* Eastw. and *A. cushingiana* Eastw. We believe there are a number of traits that reflect a close relationship and a common origin, which justifies including both in *A. glandulosa*. These traits are: the basal burl, predominantly isofacial leaves, small fruits with mealy mesocarp and separable endocarp segments, and a high frequency of populations with foliaceous bracts, although

TABLE 4. FRUIT COMPARIONS BETWEEN *A. GLANDULOSA* POPULATIONS AND *A. PARRYANA* SUBSPECIES. Three populations of the former species from the interior region of the San Gabriel Mountains, Los Angeles Co. are suspected to be of hybrid origin with *A. parryana.* The range of variation in *A. glandulosa* is illustrated by the population outside this region with the smallest (B8) and largest (C5) fruits; see Table 3 for further details on *A. glandulosa* populations.

		Fruit characters					
Population	Location	Mass (mg)	Height (mm)	Width/ height ratio	Endocarp segments	Single stone (%)	Apiculate (1–5)
A. glandulosa							
B8	Del Mar Coastal San Diego	100	4.6	1.6	4.4	0	2.8
C5	Santa Ana River San Bernardino Mtns.	373	7.6	1.3	3.2	5	3.1
B11	Glendora Ridge Interior San Gabriel Mtns.	360	8.6	1.2	2.4	32	3.7
B16	Pacifico Pk Interior San Gabriel Mtns.	409	8.2	1.3	2.1	32	3.3
B19	Mill Creek Summit Interior San Gabriel Mtns.	495	9.9	1.2	2.0	35	4.0
A. parryana							
subsp. *parryana*	Santa Ynez Mtns. (n=58)	329	9.4	1.0	1.1	93	4.3
subsp. *tumescens*	San Bernardino Mtns(n=31)	424	10.4	1.0	1.1	97	4.2

TABLE 5. *ARCTOSTAPHYLOS GLANDULOSA* SUBSPECIES AS TREATED IN THIS STUDY ALONG WITH A BRIEF TAXONOMIC HISTORY OF THEIR TREATMENT AND SYNONOMY. See text for more details.

This treatment	As named	Date	Author	Changes in status
subsp. *glandulosa*	*A. glandulosa*	1897	Eastwood	
		1939	Adams ex. McMinn	var. *glandulosa*
		1968	Wells	subsp. *glandulosa*
	A. intricata	1901	Howell	
	A. zacaenis	1933	Eastwood	
		1939	Adams ex. McMinn	var. *zacaensis*
		1968	Wells	subsp. *zacaensis*
	var. *australis*	1940	Adams	
	A. nitens	1945	Eastwood	
subsp. *leucophylla*	subsp. *leucophylla*	2007	Keeley, Vasey & Parker	
subsp. *atumescens*	subsp. *atumescens*	2007	Keeley, Vasey & Parker	
subsp. *cushingiana*	*A. cushingiana*	1933	Eastwood	
	A. howellii	1933	Eastwood	
		1939	Adams ex. McMinn	var. *cushingiana*
		2007	Keeley, Vasey & Parker	subsp. *cushingiana*
subsp. *crassifolia*	var. *crassifolia*	1922	Jepson	
		1925	Jepson	*A. tomentosa* (Pursh) Lindley var. *crassifolia*
		1968	Wells	subsp. *crassfolia*
subsp. *erecta*	subsp. *erecta*	2007	Keeley, Vasey & Parker	
subsp. *adamsii*	var. *adamsii*	1958	Munz	
		1974	Munz	subsp. *adamsii*
subsp. *gabrielensis*	*A. gabrielensis*	1992	Wells	
		2007	Keeley, Vasey & Parker	subsp. *gabrielensis*
subsp. *mollis*	var. *mollis*	1940	Adams	
		1968	Wells	subsp. *mollis*
	subsp. *glaucamollis*	1987	Wells	

bract size is variable in both glandular and non-glandular populations. In addition, in some parts of the range glandular and non-glandular plants form mixed populations that combine traits of both taxa, and we have the impression that such populations are more common than suspected hybrids between distinct species in the genus. Here we treat these two taxa as *A. glandulosa* Eastw. subsp. *glandulosa* (henceforth referred to as the nominate subspecies) and **A. glandulosa** Eastw. subsp. **cushingiana** (Eastw.) Keeley, Vasey & Parker, comb. nov. (Table 5). These taxa separate out along complex environmental gradients involving latitude, elevation and distance from the coast. In some regions their distribution is easily delineated; for example, in San Luis Obispo Co. the nominate subspecies is apparently restricted to the coastal foothills and *A. glandulosa* subsp. *cushingiana* is restricted to the higher interior ranges (Hoover 1970; J. Keeley personal observations). However, this pattern is not universal as further north from Marin Co. to Mendocino Co. the latter taxon is often found near the coast (e.g., B26 and B27). In both the glandular and non-glandular forms we find additional variation that is distinct and geographically constrained and treat these variants as additional subspecies. These, along with their taxonomic history are summarized in Table 5.

Glandular Subspecies

Most glandular populations (Group **A**) fall within the nominate subspecies, but two variations are recognized at the subspecies level. One is an intensely glaucous-leaved shrub that in other respects resembles the nominate subspecies (Fig. 4) and is here named **A. glandulosa** Eastw. subsp. **leucophylla** Keeley, Vasey & Parker, subsp. nov. These very white-leaved plants superficially resemble the non-glandular *A. glandulosa* Eastw. subsp. *adamsii* (Munz) Wells but have glandular hairs and most commonly have foliaceous bracts. This taxon is intensely glaucous like some of the plants in the type population of *A. zacaensis* Eastw. However, it is very unlike *A. glandulosa* Eastw. subsp. *zacaensis* (Eastw.) Wells, which was circumscribed as either glandular or non-glandular and with any degree of glaucous wax (Wells 1987, 2000a). Many populations in the southern half of the state that Wells considered to be *A. glandulosa* subsp. *zacaensis* are indistinguishable from the nominate subspecies, therefore we have purged that name from *Arctostaphylos* nomenclature. In the present study *A. glandulosa subsp. leucophylla* is represented by two populations, one from Cerro Bolo Peak in Baja California (A3, Fig. 4) and one from the north side of Palomar Mountain in San

Diego Co. (A16). Other populations close to this taxon (Fig. 4) and perhaps appropriately considered under this name are A14 from the east side of Palomar Mountain and A18, further west in Rancho California, Riverside Co.

A second glandular taxon that we recognize is a non-burl forming population from a mountain south of Punta Banda, Baja California, **A. glandulosa** Eastw. subsp. **atumescens** Keeley, Vasey & Parker, subsp. nov. This is a very localized population dominated by non-burl forming shrubs, probably covering only a few hectares, but in light of the near universal presence of a burl and resprouting ability in *A. glandulosa*, this unique population is considered worthy of formal recognition. The full range of this subspecies is unknown and needs further work as non-burl forming populations of *A. glandulosa* have been reported further south near San Vincente (Philip Rundel, personal communication, May 2006).

Non-Glandular Subspecies

Non-glandular taxa are characterized by short-canescent or tomentose branchlets without (Group B) or with (Group C) long villous or setose hairs. Plants lacking these long hairs are the most common non-glandular form and *A. glandulosa* Eastw. subsp. *cushingiana* (Eastw.) Keeley, Vasey & Parker is the most widespread of these, being found throughout the latitudinal range of the species.

In the southern part of the range we recognize four other non-glandular non-setose tomentose subspecies. One of these *A. glandulosa* Eastw. subsp. *crassifolia* (Jepson) Wells (populations B8, B9, and B10, Fig. 5) is a long established taxon from coastal San Diego Co. Interestingly this taxon has been readily accepted by many investigators (except Eastwood and Knight), yet it has not been described in terms that are very unique within the species. Jepson (1922) delineated it on the morphological basis that it had thick leaves, a trait shared with other populations of the species, and Adams (1940) described it based on its dark green leaves, a trait that is not unique to these coastal populations of *A. glandulosa*. We believe the primary reason for its ready acceptance as a subspecies worthy of recognition is that it has a close association with coastal terraces, atypical for *A. glandulosa*, and its non-glandular branchlets, which contrasts with the nearest conspecific populations of the glandular nominate subspecies not far inland (e.g., Escondido, A10, Table 3). However, a trait largely over-looked by *Arctostaphylos* specialists (except Wiggins 1980), but evident in our analysis, is the presence of small and markedly flattened fruits. As for distribution, this taxon is restricted to within 5 (or possibly 10) km of the coast from Encinitas south into Baja California. Wells (2000a) considered this subspecies to extend north to Carlsbad; however, our data show that many of these plants (A11) have glandular hairs, and we suggest these more northern populations represent a mixture of *A. glandulosa* subsp. *crassifolia* with the nominate subspecies. While some glandular hairs are present in the Encinitas population (B10), they only represented 5–10% of the population and our Del Mar population (B8) lacked glandular hairs.

Another non-glandular form is represented in the La Candelaria population (B1, Fig. 5) east of Ensenada, Baja California, characterized by the distinctive trait of erect nascent inflorescences. Nascent inflorescences, which persist fully formed for half a year prior to flowering, are a hallmark trait in *Arctostaphylos*; with one rare exception in *A. pringlei* (Keeley 1997, Vasey and Parker 1999, c.f. Wells 1999). In the vast majority of species these nascent inflorescences are pendant and that is the typical condition in *A. glandulosa*. The La Candelaria populations share this erect trait with two other Baja California species, *A. australis* Eastw. and *A. moranii* Wells, and the southern San Diego Co. *A. otayensis* Wieslander and Schreiber. Because this characteristic was previously unknown from *A. glandulosa*, these populations are named **A. glandulosa** Eastw. subsp. **erecta** Keeley, Vasey & Parker subsp. nov.

A non-glandular glabrous-leaved plant with highly reduced deltoid-acuminate bracts (B3, B4, B5 and B7, Fig. 5) is the subspecies originally named by Munz, *A. glandulosa* Eastw. subsp. *adamsii* (Munz) Wells. We follow the original description by Munz (1958) and reject the *sensu lato* treatment by Wells (1987, 2000a), who expanded this subspecies to include populations with glandular hairs and foliaceous bracts. In our treatment, intensely glaucous leaved plants fall into one of two subspecies, largely dependent on the presence or absence of glandular branchlets. Intensely glaucous-leaved plants with glandular branchlets, and often with foliaceous bracts, falls within *A. glandulosa* subsp. *leucophylla* Keeley, Vasey & Parker, whereas non-glandular intensely glaucous plants with highly reduced bracts are *A. glandulosa* subsp. *adamsii.*

The other non-glandular tomentose subspecies has bright green somewhat lustrous leaves, with reduced bracts and has a greater degree of nutlet fusion than in other *A. glandulosa* taxa (B11, B13, B14, B15, B16, B17, B18, B19, and B24, Fig. 6). Some individual plants produce a solid stone (Table 3), but most plants have 2–3 endocarp segments, with some individuals in all populations ranging from 1–4 segments. This taxon subsumes *A. gabrielensis* Wells, and here is treated as **A. glandulosa** Eastw. subsp. **gabrielensis** (Wells) Keeley, Vasey, & Parker, comb. nov.

Lastly, of the non-glandular forms, we recognize only one taxon with long setose or villous

hairs, *A. glandulosa* Eastw. subsp. *mollis* (Adams) Wells. We do not recognize *A. glandulosa* Eastw. subsp. *glaucomollis* (Eastw.) Wells as a separate entity due to the lack of any clear geographical distribution of foliaceous and scale-like bracts (Fig. 7) as proposed by Wells (1987, 2000a).

Key to *Arctostaphylos Glandulosa* Subspecies

1. Branchlets with glandular hairs and bracts mostly foliaceous
   2. Leaves scabrous with non-glaucous to moderate glaucous bloom
      3. Basal burl present (Baja to Oregon) . . . . . subsp. *glandulosa*
      3′ Basal burl absent (N. Baja) . . . . . subsp. **atumescens**
   2′ Leaves with intensely glaucous bloom (interior southern California) . . . . . subsp. **leucophylla**

1′ Branchlets lacking glandular hairs, sometimes slightly viscid inflorescence
   4. Branchlets short-villous, tomentose or puberulent, leaves glabrate to moderately tomentose
      5. Leaves slightly pubescent yellow-green to dark green, lower inflorescence bracts foliaceous or reduced
         6. Nascent inflorescences pendant
            7. Fruits slightly flattened, leaves green or gray-green (Baja to Oregon) . . . . subsp. **cushingiana**
            7′ Fruits markedly flattened, leaves dark green, leaf margins sometimes reddish (coastal San Diego Co.) . . . . . subsp. *crassifolia*
         6′ Nascent inflorescences erect (n. Baja) . . . . . subsp. **erecta**
      5′ Leaves glabrate and intensely dull white or highly lustrous green, lower inflorescence bracts mostly reduced or absent
         8. Leaves intensely glaucous, fruit endocarp 2–4 segments (interior San Diego Co. and n. Baja) . . . . . subsp. *adamsii*
         8′ Leaves bright lustrous green, fruit endocarp 1–2 segments of fused nutlets (interior San Gabriel Mountains, Sierra Madre Mountains) . . . . . subsp. **gabrielensis**
   4′ Branchlets pubescent to almost glabrate but with long setose or villous hairs, bracts variable, plants in the western portion of the range with upper leaf surface somewhat lustrous and having substantially fewer stomata than the lower surface (South Coast and Transverse ranges, occasionally further south) . . . . . subsp. *mollis*

Arctostaphylos glandulosa Eastw. subsp. *glandulosa* (Eastw.) Wells, Eastwood Manzanita, Proc. Cal. Acad. Sci. ser. 3, 1:82. 1897. *A. intricata* Howell, Fl. NW. Amer., Vol. I, 417, 1901. *A. zacaensis* Eastw., Leafl. West. Bot. 1:79, 1933. *A. glandulosa* Eastw. var. *zacaensis* (Eastw.) Adams ex McMinn, Illus. Manual Calif. Shrubs 417, 1939. *A. glandulosa* Eastw. subsp. *zacaensis* (Eastw.) Wells, Madroño 19:205, 1968. *A. glandulosa* Eastw. var. *howellii* (Eastw.) Adams ex McMinn, Illus. Manual Calif. Shrubs 417, 1939. *A. glandulosa* Eastw. subsp. *howellii* (Eastw.) Wells, Madroño 19:205, 1968. *A. glandulosa* Eastw. var. *australis* Adams, J. Elisha Mitchell Sci. Soc. 56:51, 1940. *A. nitens* Eastw. Leafl. West. Bot. 4:148, 1945. — SYNTYPE: USA, California, Marin Co., Mt. Tamalpais, 5 March 1922, *A. Eastwood 11078* (holotype, CAS).

Evergreen shrub with pendulous nascent inflorescences appearing in the late spring and summer prior to the following winter flowering season and with a swollen basal lignotuber with dormant buds that initiate growth after fire. Isofacial leaf anatomy with well-developed palisade tissue on both sides and abundant stomata on both the upper and lower leaf surfaces, scabrous and dark green with or without light glaucous bloom, indument of short to long hairs, many with glands, nascent inflorescences usually with lower bracts foliaceous, but sometimes all bracts reduced, and depressed fruits with width greater than height, mealy endocarp, and nutlets separable into 2–5 segments.

Distribution: Coastal mountains from northern Baja California to Oregon.

Epithet etymology: The epithet refers to the glandular hairs on branchlets, rachises, and sometimes pedicels and fruits.

Arctostaphylos glandulosa Eastw. subsp. **atumescens** Keeley, Vasey & Parker, subsp. nov. — TYPE: MEXICO, Baja California, north-facing slopes along dirt road between Cerro El Cantil and Cerro Buenavista, southwest of Punta Banda, 610 m, 31°40′ N, 116°36′ W, 26 Aug 1993, *J.E. Keeley, A. Massihi, & C.J. Fotheringham 24160* (holotype, RSA; isotypes, CAS, ENS, SD, UC).

A. glandulosa Eastw. subsp. *glandulosa* lignotubere deficienti et non repullulans post ignem differt.

Differing from the nominate subspecies by lacking a lignotuber and not resprouting after fire.

Distribution: Type locality only confirmed location.

Epithet etymology: Refers to the lack of a basal burl, a unique characteristic in this species.

Arctostaphylos glandulosa Eastw. subsp. **leucophylla** Keeley, Vasey & Parker, subsp. nov. — TYPE: USA, California, San Diego Co., Heliport on northeastern face of Palomar Mountain., on road to High Point, 9.3 km

southwest of Hwy 79, 33°20′, 116°47′ W, 1505 m elevation, 18 Sept 1992, *J.E. Keeley 21289* (holotype, RSA; isotypes, CAS, UCB, SD, ENS).

A. glandulosa subsp. *glandulosa* foliis glaucis maxime differt.

Differing from the nominate subspecies by extremely glaucous leaves.

Paratypes: MEXICO, Baja California, steep slopes in vicinity of Nativos de Vaille, above road to Punta Cabras, 15 km south of Santa Tomás, 400 m, 4 Aug 1993, *A. Massihi, S.A. Hirales, & J.E. Keeley 23809* (RSA); Baja California, Cerro Bolo Peak, 1220 m, 32°19′, 25 July 1993, *J.E. Keeley 23440* (RSA); USA, California, San Diego Co., along Old Ranch Rd., 1 km southwest of Hwy. 8 at Japutal Valley, 1040 m, 8 Aug. 1993, *J.E. Keeley 24038* (RSA); chaparral northwest of intersection between Japutal Valley Rd. and Lawson Truck Trail, 700 m, 6 Sept 1975, *J.E. Keeley 5879* (RSA); along Mother Grundy truck trail, 1 km south of Honey Springs Rd., 600 m, 8 Aug. 1993, *J.E. Keeley 24013* (RSA); Los Pinos Peak, northwest of Lake Moreno on 16S17, 1460 m, 8 Aug 1993, *J.E. Keeley 24060* (RSA); north-facing slope of Guatay Peak, 1120 m, 8 Aug 1993, *Keeley 24,051* (RSA); Flinn Ranch (Kitchen Creek) Rd., 15 km north of Old Hwy 80, southern Laguna Mountains., 1590 m, 17 Aug 1992, *J.E. Keeley, A. Massihi, & R. Gore 18906* (RSA); Riverside Co., rock outcrop Red Mountain. Rd./Stanely Rd., 11.7 km east of R3, 975 m, 16 July 1992, *J.E. Keeley 16587* (RSA); Hwy 234, 3 km north of Hwy 74, San Jacinto Mountains., 1520 m, 16 June 1992, *J.E. Keeley 16819* (RSA).

Distribution: Away from the coast often on gabbro or basaltic soils in southern California and northern Baja California.

Epithet etymology: This epithet refers to the intensely white glaucous leaves.

Arctostaphylos glandulosa Eastw. subsp. **cushingiana** (Eastw.) Keeley, Vasey & Parker, comb. nov. *A. cushingiana* Eastw., Leafl. West. Bot. 1:75, 1933. *A. howellii* Eastw., Leafl. West. Bot. 1:123, 1934. *A. glandulosa* Eastw. var. *cushingiana* (Eastw.) Adams ex McMinn, Illus. Manual Calif. Shrubs 417, 1939. — TYPE: USA, California, Marin Co., south side of Mt. Tamalpais, 12 March 1922, *A. Eastwood 11075A* (holotype, CAS).

Lacking glandular hairs. Branchlets with short hairs, puberulent or tomentose. Occasional populations included here may have glands on inflorescences and/or fruits.

Distribution: From northern Baja California to northern California (perhaps Oregon). In the south mostly on interior sites.

Epithet etymology: This epithet honors Sidney Cushing, someone "who during his life, identified with Mount Tamalpais" (Eastwood 1933).

Arctostaphylos glandulosa Eastw. subsp. *crassifolia* (Jepson) Wells, Madroño 19:205, 1968. *A. glandulosa* Eastw. var. *crassifolia* Jepson, Madroño 1:86, 1922. *A. tomentosa* (Pursh) Lindley var. *crassifolia* (Jepson) Jepson, Manual fl. Plants Calif. 749, 1925. — TYPE: USA, California, San Diego Co., sandy mesas at Del Mar, 9 June 1901 *W.L. Jepson 1606a* (holotype, UC).

Lacking glandular hairs. Branchlet and nascent indument tomentose to short villous. Leaves dark green, sometimes with a reddish margin. Fruits markedly more flattened than other subspecies.

Distribution: Coastal sandstone substrates from north of Encinitas in San Diego County south to near Erendira, Baja California.

Epithet etymology: The epithet recognizes the somewhat thicker leaves on this taxon.

Arctostaphylos glandulosa Eastw. subsp. **erecta** Keeley, Vasey & Parker, subsp. nov. — TYPE: MEXICO, Baja California, foothills 32 km east of Ensenada in foothills along Hwy 3, 600 m, 31°53′ N, 116°19′ W, 24 July 1992, *J.E. Keeley, A. Massihi, & R. Goar 17927* (holotype, RSA; isotypes, CAS, ENS, SD, UC).

Trichomata glanduliferis deficientia. Ramuli tomentosi. Inflorescentiae nascentes erectae.

Glandular trichomes absent; branchlets tomentose. Nascent inflorescensces erect.

Distribution: Foothills at the southwestern end of the Sierra Juarez Mountains in northern Baja California.

Arctostaphylos. glandulosa Eastw. subsp. *adamsii* (Munz) Munz, Flora S. Calif. 400, 1974. *A. glandulosa* Eastw. var. *adamsii* Munz, Aliso 4:95, 1958. — TYPE: USA, California, San Diego Co., northern end of the Laguna Mtns. along road to Julian, 20 Aug 1942, *P.A. Munz & E.K. Balls 17958* (holotype, RSA).

Lacking glandular hairs or other long hairs, branchlets tomentulose to tomentose. Leaves glabrous, dull and densely glaucous. Nascent bracts reduced deltoid.

Distribution: Interior edge of chaparral in San Diego County south into interior northern Baja California.

Epithet etymology: This epithet honors J.E. Adams, one of the important 20th century students of the genus and whose Ph.D. dissertation was the standard treatment for *Arctostaphylos* during most of the latter two-thirds of the century.

Arctostaphylos glandulosa Eastw. subsp. **gabrielensis** (Wells) Keeley, Vasey & Parker, comb. nov., *A. gabrielensis* Wells, Four Seasons 9(2):46–47, 1992. — TYPE: USA, California, Los Angeles Co., San Gabriel Mountains, Mill Creek Summit, 1470 m, 10 March 1986, *P. V. Wells & J.E. Keeley 31086* (holotype, CAS).

Lacking glandular hairs, branchlets tomentulose, leaves glabrous, lustrous and bright green. Nascent bracts reduced deltoid and fruits similar to the nominate subspecies in shape but larger often reddish pericarp and more leathery mesocarp and with a tendency for nutlets to coalescence into 1–2 (4) segments of one or more druplets.

Paratypes: USA, California, Los Angeles, Co, Glendora Ridge Rd., 6 km southwest of Baldy Rd., 1410 m, 15 Oct 1992, *J.E. Keeley & M.B. Keeley 22122* (RSA); Singing Pines Camp, Angeles Crest Hwy, 2000 m, 2 Sept 1978, *J.E. Keeley 7226* (RSA); south-facing slopes at end of Hwy 39, northwest of Crystal Lake, 1720 m, 15 Oct 1992, *J.E. Keeley 22101* (RSA); Santa Barbara Co., Sierra Madre Rd, 13 km west of McPherson Peak, Sierra Madre Mountains, 1690 m, 7 Aug. 1992, *J.E. Keeley & M.B. Keeley 19017* (RSA).

Distribution: Mostly interior portions of the San Gabriel Mountains, Los Angeles Co., occurring in disjunct populations as far north as the Sierra Madre Mountains, Santa Barbara Co.

Epithet etymology: The epithet reflects the distribution of this subspecies is largely in the San Gabriel Mountains.

Arctostaphylos glandulosa Eastw. subsp. *mollis* (Adams) Wells, Madroño 19:205, 1968. *A. glandulosa* Eastw. var. *mollis* Adams, J. Elisha Mitchell Sci. Soc. 56:50, 1940. *A. glandulosa* Eastw. subsp. *glaucomollis* Wells, Four Seasons 7(4):20, 1987. — TYPE: USA, California, Santa Barbara Co., La Cumbre Peak, Santa Ynez Mountains, 20 Feb 1935, *J.E. Adams 954* (holotype, UC).

Lacking glandular hairs. Branchlets with short hairs, puberulent or tomentose and with long villous hairs. Occasional populations included here may have glands on inflorescences and/or fruits. Throughout the range bract size varies from foliaceous to reduced.

Distribution: South Coast and Transverse ranges and occasional populations in the Peninsular Ranges and coastal mountains of San Diego and Baja California.

Epithet etymology: Refers to the long soft flexible hairs.

Discussion

Arctostaphylos glandulosa Eastw. is a wide ranging tetraploid species circumscribed as having isofacial leaves with stomata on both leaf surfaces, indument with short or long hairs, glandular or non-glandular branchlets, pendant nascent inflorescences, depressed-globose fruits usually with separable endocarp segments of several nutlets, and a basal burl. This study has shown that there is some population level variation in many of these traits, including populations with markedly bifacial leaves, or with erect nascent inflorescences, or a tendency towards solid stones and even one population lacking a basal burl. Many of these population level characteristics vary in geographically predictable patterns and should be given taxonomic recognition.

Subspecific variation is dominated by two widely distributed morphotypes, the glandular nominate subspecies and the non-glandular short pubescence *A. glandulosa* Eastw. subsp. *cushingiana* (Eastw.) Keeley, Vasey and Parker. In addition, seven other subspecies of more localized distribution are recognized, largely concentrated in southern California and Baja California. These subspecies are based on phenetic patterns of variation and represent relatively monomorphic allopatric populations. Where these taxa meet, mixed populations may occur.

Any taxonomic treatment assumes that all populations of a given taxon have a common origin. In highly localized subspecies of *A. glandulosa* there is far less reason to question that assumption than for wide ranging subspecies, some of which require critical evaluation. For example, Wells (1987, 2000a) considered any level of glaucous bloom on leaves of plants from central and southern California constituted *A. glandulosa* subsp. *zacaensis* and the origin of this trait was due to hybridization with *A. glauca*. However, Wells' circumscription of *A. glandulosa* subsp. *zacaensis* comprised a wide diversity of populations with slight to moderate glaucous bloom, over a huge distributional range. Here we do not recognize that taxon because the presence of any amount of glaucousness on the leaf is potentially a trait of diverse origins throughout the range. The numerous demonstrated cases of hybridization in *Arctostaphylos* (Dobzhansky 1953, Howell 1955, Gottlieb 1968, Keeley 1976, Kruckeberg 1977, Ellstrand et al. 1987), and the number of intensely glaucous-leaved species found throughout the range that could be potential contributors to the glaucous foliage, provide justification for questioning that taxon. This decision also eliminates major problems in correctly classifying many populations within the range Wells (1987, 2000a) circumscribed for *A. glandulosa* subsp. *zacaensis.* For example, all glandular plants south of San Francisco were considered to be this taxon yet our analysis revealed three populations (A12, A13, and A6, Fig. 4) in southern California that were distinctly non-glaucous.

Understanding patterns of variation in *A. glandulosa* requires some evaluation of the palaeohistory of vegetation distribution in this region. Over most of the last 2 million years conditions throughout the area now characterized as the California Floristic Province were cooler and wetter than today, and thus the contemporary plant distribution is not likely more than 10,000 years old. Prior to this many chaparral taxa such as *Arctostaphylos* were distributed much further south or lower in elevation (Axelrod 1950; Raven and Axelrod 1978; Wells 2000b; Rhode 2002). Holocene climate changes resulted in migration that followed unique patterns for different taxa, potentially bringing together populations long isolated from one another. These conditions likely set the stage for potential hybridization and introgression of genetic variation from previously isolated *Arctostaphylos* taxa and form the basis for Wells (2000a) model of "reticulate evolution" in the genus. While many aspects of this model are likely true, it tends to downplay the potential role for strong directional selection under the changing climatic conditions of the Holocene. These two models of course are not mutually exclusive and likely have worked in concert to generate contemporary patterns of subspecific variation in *A. glandulosa.*

The role of hybridization has been considered by Wells (2000a) to have been of immense importance in the evolution of *Arctostaphylos* and he speculated on numerous hybridization events involving *A. glandulosa*. Several factors complicate such evaluations. Claims of hybridization by Wells (2000a) were based on the presence of shared traits and often unwarranted assumptions about the direction of gene transfer from one taxon to another. In addition these hybrid claims were markedly influenced by the current overlap in species ranges. This latter factor is particularly troubling because of the distinct possibility that the origin of subspecific variation within *A. glandulosa*, or any other species, may not be recent, and some of it could predate the current distribution patterns of related taxa. For example, Wells (1987, 2000a) claimed that *A. campbellae* was a hybrid between *A. crustacea* and *A. glauca*, but based on patterns of phenetic variation (Fig. 2) there is good reason to discount involvement of the latter species in the origin of *A. campbellae*. Indeed, if hybridization were involved, patterns of morphological similarity would favor *A. glandulosa* as one of the parents (Fig. 2). Apparently the presence of *A. glauca* in the vicinity and absence of *A. glandulosa* from the region led to Wells' unlikely conclusion about the origin of *A. campbellae*. Of course there is no reason to *a priori* assume hybridization is the driver behind this particular taxon and an equally plausible hypothesis is that directional selection in *A. crustacea* has selected for decreased bifaciality of leaves and other changes of selective value on the drier more interior slopes of Mt. Hamilton and San Antonio Valley in Santa Clara County. This directional selection model may be what McMinn (1939) and Adams (1940) had in mind when they hypothesized that *A. crustacea* was a likely intermediate stage between the coastal *A. tomentosa* and the interior *A. glandulosa*. Consistent with this model is the morphological similarity of *A. campbellae* and *A. glandulosa* subsp. *mollis*; similar in that both are non-glandular with long villous hairs. These taxa differ largely in their relative placement on a scale from bifacial to isofacial leaves, with the latter taxon falling somewhere between *A. campbellae* and other *A. glandulosa* subspecies.

Future molecular studies may help resolve some of the unknowns about the origins of variation in *Arctostaphylos glandulosa*. However, interpreting both morphological and molecular data will require a better understanding of how to detect pathways of reticulate evolution resulting from hybridization and introgression and how to distinguish this from directional selection along environmental gradients.

Conclusions

This study clarifies some ambiguity and confusion in the most recent classification of subspecific variation in *A. glandulosa* (Wells 2000a). In our treatment the nominate subspecies has been restored as the dominant glandular taxon throughout the range of the species. A new combination was made to include most non-glandular pubescent populations, *A. glandulosa* subsp. *cushingiana.* Two subspecies, *A. glandulosa* subsp. *crassifolia*, and *A. glandulosa* subsp. *adamsii*, which had been re-described by Wells to circumscribe a wider range of variation, were returned to taxa more closely approximating the type specimen. This treatment of the latter taxon required describing a new subspecies, *A. glandulosa* subsp. *leucophylla*, for glandular plants with intensely glaucous leaves. One species, *A. gabrielensis* was subsumed under *A. glandulosa* subsp. *gabrielensis*. The former subspecies *A. glandulosa* subsp. *glaucomollis* was subsumed under *A. glandulosa* subsp. *mollis.* Two new localized subspecies from Baja California are named, *A. glandulosa* subsp. *atumescens*, similar to the nominate subspecies but is a uniquely non-burl forming taxon, and *A. glandulosa* subsp. *erecta*, a non-glandular taxon with erect nascent inflorescences.

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NEW COMBINATIONS IN NORTH AMERICAN *LATHYRUS* AND *VICIA* (FABACEAE: FABOIDEAE: FABEAE)

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ABSTRACT

Morphological and geographic variation in two *Lathyrus* and two *Vicia* species complexes is reviewed. The following new combinations are proposed: **Lathyrus nevadensis** S. Wats. var. **cusickii** (S. Wats.) Broich comb. nov., **Lathyrus lanszwertii** Kellogg var. **sandbergii** (T. White) Broich comb. nov., **Vicia ludoviciana** Nutt. ex T. & G. var. **leavenworthii** (T. & G.) Broich comb. nov., and **Vicia nigricans** H. & A. var. **gigantea** (Hooker) Broich comb. nov.

Key Words: Fabaceae, *Lathyrus*, *Vicia*, Leguminosae, Vicieae, taxonomic changes.

Lathyrus L. and *Vicia* L. (Fabaceae: Faboideae: Fabae [Vicieae]) are sister genera of papilionoid legumes each of about 150 species. *Lathyrus* in North America was last revised by Hitchcock (1952), and *Vicia* by Hermann (1960). Isely (1998) has summarized more recent taxonomic changes in both genera. Preparation of treatments of *Lathyrus* and *Vicia* for the *Flora of North America* has given me the opportunity to re-examine the taxonomy of both genera. As a result of this research, I propose taxonomic changes within two native *Lathyrus* species complexes and two nomenclatural transfers within *Vicia* so that all infra-specific *Vicia* taxa in North America be treated uniformly at the varietal level. The purpose of this communication is to describe the morphological and geographic variability within each of these species complexes and to publish four new nomenclatural combinations.

LATHYRUS NEVADENSIS S. WATS.

Lathyrus nevadensis s.l. occurs along the Pacific Coast of North America west of the Sierra-Cascade axis from Fresno Co., California, north to British Columbia and east of the Cascades in central and northeast Oregon, central Washington, and east into the Idaho panhandle. Chromosome evidence accumulated to date (Hitchcock 1952; Broich 1989) suggests that *L. nevadensis* is tetraploid at $2n = 28$. Three varieties including five races occur within this range (Table 1, Fig. 1): var. *nevadensis*, var *parkeri* (St. John) C. L. Hitchcock, and var. *cusickii* (T. White) Broich comb. nov.

Lathyrus nevadensis var. *nevadensis* includes two races. One race consists of short (<3 dm), erect plants bearing 4–6 leaflets on leaf rachises ending in, at most, a short (<1 cm) bristle rather than a tendril, and with 2–4(6)-flowered racemes of rather large (15–20 mm) flowers (*L. nevadensis s.s.*). A second race consists of sprawling or clambering plants up to 6 dm tall bearing leaves of 6–8(10) leaflets on rachises which end in a long, (>2 cm), often branched and prehensile tendril, and with racemes of 4–8 smaller (10–17 mm) flowers (*L. lanceolatus* Howell). The nevadensis race is more common in the southwestern part of the range from Fresno Co., California, north into the coast range forests of western Oregon; the lanceolatus race found throughout the range of the variety (Fig. 1) but is more common to the north and in the eastern foothills of the Cascades in central Washington.

In northwestern California and southwestern Oregon, the nevadensis race intergrades so completely with the lanceolatus race that some populations (or plants within populations) can be only arbitrarily assigned to one race or the other. Hitchcock (1952) noted this intergradation but maintained the two forms as separate subspecies (subsp. *nevadensis* and subsp. *lanceolatus* (Howell) C. L. Hitchcock). Isely (1992) concluded that the entire series of populations included in the two subspecies recognized by Hitchcock is best treated as one variety, var. *nevadensis*.

An analogous situation exists in northeast Oregon, southwest Washington, and adjacent Idaho. In the southern part of this range, there are populations of *Lathyrus* rather similar to the nevadensis race of *L. nevadensis* (as described above) but with white rather than blue flowers. Originally described as *L. cusickii* S. Wats., Hitchcock (1952) recognized these populations as *L. nevadensis* subsp. *cusickii* (S. Wats.) C. L. Hitchcock. In northern Idaho, there are white flowered populations vegetatively similar to the lanceolatus race of *L. nevadensis*. Described as *Lathyrus parkeri* St. John, Hitchcock (1952) recognized these populations as *L. nevadensis* subsp. *lanceolatus* var. *parkeri* C. L. Hitchcock.

TABLE 1. A KEY TO AND DESCRIPTIONS OF THE VARIETIES OF *LATHYRUS NEVADENSIS* S. WATS. S. L.

Variety	Race [*1]	Plant height (dm)	Plant habit	Rachis length (cm)	Tendrils	Number of leaflets	Leaflet shape
1. Corollas blue-purple, wings lighter; plants of California, western Oregon, or western and central Washington							
nevadensis [*2]	*nevadensis*	1–3	erect	2–5(6)	aristate	4–6	ovate to lanceolate
nevadensis [*2]	*lanceolatus*	3–6	sprawling or climbing	4–10	long, branched, prehensil	6–8(10)	ovate to lanceolate
1. Corollas white; plants of northeastern Oregon, extreme eastern Washington and Idaho							
2. Leaf rachis 4–9 cm, leaflets 6–10, tendrils well developed; flowers, 5–10, 12–18 mm long							
parkeri [*3]		2–6	sprawling or climbing	5–10	long, branched, prehensil	6–8(12)	ovate to lanceolate
2. Leaf rachis 2–5 cm, leaflets 4–6, tendrils reduced to bristles usually less than 1 cm long; flowers 2–4, 18–22 mm long.							
cusickii [*4]	broad leaflet	2–4	erect	2–5(7)	aristate	2–6	ovate to lanceolate
cusickii [*4]	narrow leaflet	2–4	erect	2–5(7)	aristate	2–6	linear

[*1] Details of racial differences and relationships are given in the text Description and distrubution based on examination of:
[*2] 567 specimens examined from WS, WTU, HSU, NY, RM, OSC, ORE.
[*3] 82 specimens examined from WS, WTU, NY, OSC, ORE.
[*4] 111 specimens examined from WS, WTU, NY, OSC, OR.

Isely (1992) merged these eastern white flowered forms into one variety — *L. nevadensis* var. *parkeri* (St. John) C. L. Hitchcock. However, there is little evidence of intergradation between the *parkeri* and *cusickii* forms in the region and I believe it is more appropriate to treat the white flowered variants of *L. nevadensis s.l.* as separate varieties: var. *parkeri* (St. John) C. L. Hitchcock and var. *cusickii* (T. White) Broich comb. nov.

Lathyrus nevadensis var. **cusickii** (S. Wats.) Broich comb. nov. *L. cusickii* S. Wats., Proc. Amer. Acad. Arts Sci. 17:371. 1882. *L. nevadensis* subsp. *cusickii* (S. Wats.) C. L. Hitchcock, Univ. Wash. Publ. Biol. 15:44. 1952. TYPE: USA, Oregon, Union Co., dry mountain slopes, *Cusickii s.n.* (holotype GH, isotype ORE!). *Lathyrus pedunculatus* St. John, Proc. Biol. Soc. Wash. 41:195. 1928. Type: USA, Idaho, [Kootnei Co.?] Turner Creek, Lake Coeur d'Alene, *St. John et. al. 4281* (holotype WS!)

A linear-leafleted race of *Lathyrus nevadensis* var. *cusickii* exists (Table 1) and morphological intermediates between linear-leafleted and ovate-lanceolate leafleted races have been collected (*C. L. Hitchcock 18982*; Umatilla Co., Oregon; WTU!, WS!). While common in other species complexes of *Lathyrus* in North America, linear-leafleted variants have not been found elsewhere in the *L. nevadensis* complex. In addition, there have been a few blue-flowered variants of var. *cusickii* collected in the Kooteni Co., Idaho, in the Coeur d'Alene area (= *L. pedunculatus* St. John). The evolutionary significance of these collections is unknown.

LATHYRUS LANSZWERTII KELLOGG

Lathyrus lanszwertii s.l. includes a series of populations ranging east of the Sierra Nevada and Cascade Range crests from southern Arizona north to British Columbia and eastward into Idaho, Montana, Wyoming, Utah, Colorado and New Mexico (Fig. 2). *Lathyrus lanszwertii* consists of a morphologically diverse collection of populations of varying degree of distinctness. The taxonomic treatment of these populations has had a complex history (Hitchcock 1952; Welsh 1965, 1978; Welsh et al. 1987; Barneby 1989; Isely 1992, 1998). *Lathyrus lanszwertii* is known to include both diploid ($2n = 14$) and tetraploid ($2n = 28$) populations (Hitchcock 1952), but the relationship between ploidy level and the morphological, ecological, and geographic variation within the complex is unknown. As conceived here, *L. lanszwertii* consists of five intergrading morphological variants (Table 2, Fig. 2): var. *lanszwertii*, var. *aridus* (Piper) Jepson, var. *pallescens* Barneby. var. *leucanthus* (Rydb.) Dorn, and var. *sandbergii* (T. White) Broich comb. nov.

Lathyrus lanszwertii s.s. (var. *lanszwertii*) is found on eastern slopes of the Cascade Ranges and the Sierra Nevada from Washington, Oregon, and California southeast into central Utah. *Lathyrus lanszwertii* var. *aridus* (Piper) Jepson, seemingly a diminutive form of var. *lanszwertii*

TABLE 1. EXTENDED.

Leaflet length (mm)	leaflet width (mm)	Leaflet L/W ratio	Inflor-escence length (cm)	Number of flowers	Flower length (mm)	Flower color	Distribution
1. Corollas blue-purple, wings lighter; plants of California, western Oregon, or western and central Washington							
20–45	10–20	1.4–2.4	2–5	2–6	15–20	blue/ purple	w. of the Sierra-Cascades; Calif. to central Oreg.
20–45	10–20	1.7–2.3	3–7	4–8	10–17	blue/ purple	w. of the Sierra-Cascades; n. Calif. to B.C. and e. of Cascades in Wash.
1. Corollas white; plants of northeastern Oregon, extreme eastern Washington and Idaho							
2. Leaf rachis 4–9 cm, leaflets 6–10, tendrils well developed; flowers, 5–10, 12–18 mm long							
30–50	15–25	1.6–2.0	6–12	5–10	12–16	white	e. Wash. and adj. n. Idaho
2. Leaf rachis 2–5 cm, leaflets 4–6, tendrils reduced to bristles usually less than 1 cm long; flowers 2–4, 18–22 mm long.							
30–50	10–20	1.6–2.2	4–7(12)	2–5	18–22	white	ne. Oreg., se. Wash, adj. Idaho
30–120	2–5	10.0–25.0	4–7(12)	2–5	18–22	white	ne. Oreg., se. Wash, adj. Idaho

lacking tendrils, and has a similar range as var. *lanszwertii*, but is more commonly found at sites dominated by *Artemisia*.

In central Utah and to the north and east into Colorado and Wyoming populations of *Lathyrus lanszwertii* take a different appearance — shorter in stature, fewer leaflets, bearing white flowers — and have been described by Barneby (1989) as var. *pallescens* Barneby. Barneby (1989) also delimited southern Utah and northern Arizona populations of *L. lanszwertii* as var. *leucanthus* (Rydb.) Dorn, which includes two distinctly different races (formerly regarded as separate species): an ovate-lanceolate leafleted race (*L. leucanthus* Rydb. *s.s.*) and a linear leafleted race (*L. arizonicus* Britton).

To the north and east of the range of *Lathyrus lanszwertii* extralimital to Barneby's (1989) treatment of intermountain forms of *lanszwertii,* there are a series of populations traditionally treated as *L. bijugatus* T. White which are, in fact, quite similar to *L. lanszwertii* var. *leucanthus*. Morphological similarities between *L. bijugatus* and *L. lanszwertii* var. *leucanthus* are such that I believe that *L. bijugatus* should be included in *L. lanszwertii s.l.*. Given the 1500 km disjunction between these northern populations and populations of var. *leucanthus* in Arizona, Colorado, and New Mexico, I hesitate to combine all into one taxon and so herein designate an additional variety of *L. lanszwertii*. *Lathyrus lanszwertii* var. *sandbergii* Broich comb nov. that also includes two distinctly different races: an ovate leafleted race (*L. bijugatus* T. White) and a linear leafleted race (*L. bijugatus* var. *sandbergii* T. White). There appears to be no difference in geographic distribution between these two forms; possible ecotypic differences have not been investigated.

Lathyrus lanszwertii var. **sandbergii** (T. White) Broich comb. nov. *Lathyrus bujugatus* var. *sandbergii* T. White. Bull. Torrey Bot. Club 21:457. 1894. TYPE: Idaho: Latah, Co., *J. H. Sandberg in 1892* (holotype NY!). *Lathyrus bujugatus* T. White, Bull. Torrey Bot. Club 21:457. 1894. TYPE: Idaho: Latah Co., *J. H. Sandberg in 1892* (holotype NY!; isotype WS!).

Species Excluded from *Lathyrus lanszwertii* Kellogg s.l.

I exclude from my understanding of *Lathyrus lanszwertii s.l.* the following taxa sometimes allied with the complex.

Lathyrus tracyi Bradshaw. While Jepson (1936) treated *L. tracyi* of northern California as a variety of *L. bolanderi* S. Wats. (= *L. vestitus* Nutt. ex T. & G.), Isely (1992, 1998) considered *tracyi* a variety of *L. lanszwertii*. *Lathyrus tracyi* includes both ovate- and linear-leafleted forms. Linear-leafleted populations certainly suggest a relationship to *L. lanszwertii*, but ovate-leafleted forms, the presence of mid-stem branching, and floral structure suggest to me that *L. tracyi* may be better allied to *L. holochlorus* (Piper) C. L. Hitchcock found to the north in the Willamette Valley of western Oregon.

Lathyrus brownii Eastwood. Hitchcock (1952) treated *L. brownii* of eastern California as a variety of *L. pauciflorus* Fernald while Barneby (1989) treated *L. brownii* as variety of *L. lanszwertii*. I believe its affinities may lie elsewhere, perhaps with *L. parviflorus* S. Wats. in Mexico.

Lathyrus laetivirens Greene. Hitchcock (1952) treated *L. laetivirens* as a variety of *L. leucanthus*

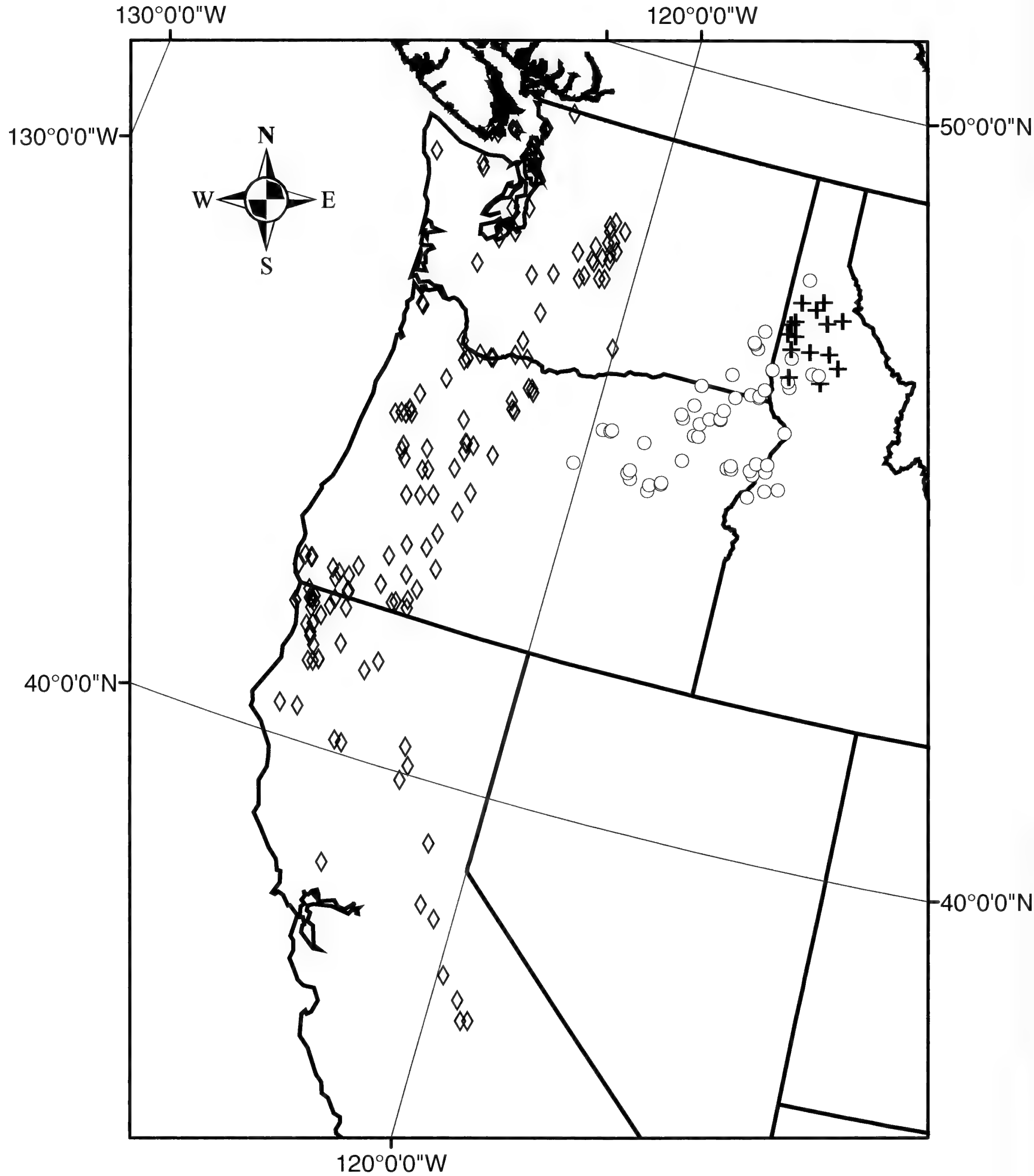

FIG. 1. Distribution of *Lathyrus nevadensis* S. Wats.: var. *nevadensis* = open diamonds; var. *cusickii* (T. White) Broich = open circles; var. *parkeri* (St. John) C. L. Hitchcock = crosses. Distribution base upon specimens from HSU, NY, ORE, OSC, WS, and WTU.

Rydb. and subsequently Welsh (1965, 1978) and Isely (1998) have included *laetivirens* within the *L. lanszwertii* complex in Utah. Barneby (1989), however, has maintained *L. laetivirens* at the specific level. I concur with Barneby. *Lathyrus lanszwertii* var. *pallescens* Barneby is distinct from *L. laetivirens* and I do not believe that the type of var. *pallescens* (Utah: Juab Co.: 20 June 1950, *A R. Kurckeberg 4496*, NY!) is referable to *L. laetivirens* as suggested by Isely (1998). Certain features of *L. laetivirens*, notably its strictly ovate leaflets and large white flowers, suggest it may be better allied with *L. nevadensis* S. Wats.

Until such time that their true relationships can be assessed more carefully, it is my belief that *Lathyrus tracyi* Bradshaw, *L. brownii* Fernald,

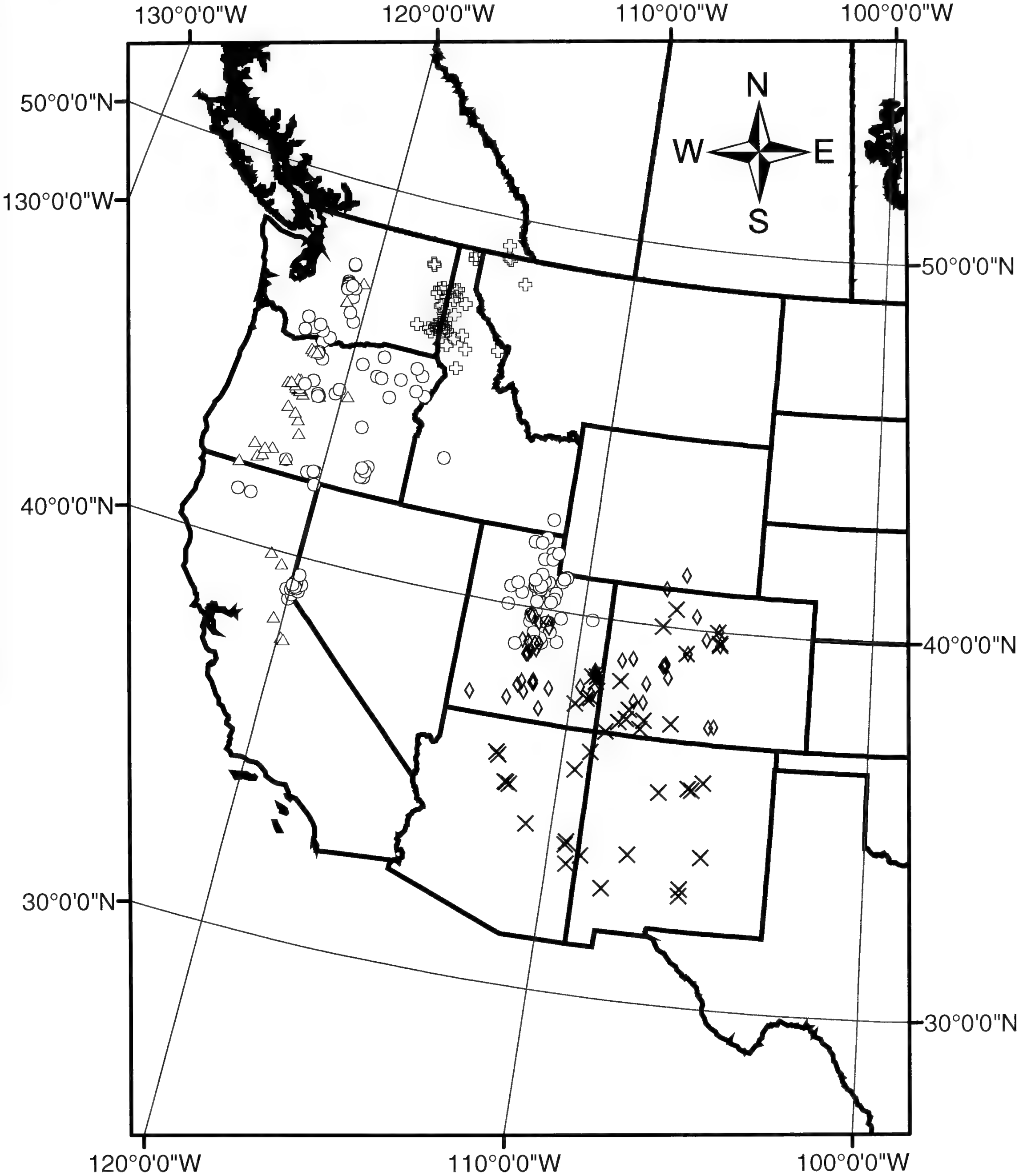

FIG. 2. Distribution of *Lathyrus lanszwertii* Kellogg: var. *lanszwertii* = open circles; var. *aridus* (Piper) Jepson = open triangles; var. *pallescens* Barneby = open diamonds; var. *leucanthus* (Rydb.) Dorn = X's; var. *sandbergii* (T. White) Broich = open crosses. Distribution base upon specimens from BRY, HSU, NY, ORE, OSC, WS, and WTU.

and *L. laetivirens* Greene be accorded specific status.

VICIA LUDOVICIANA NUTTALL IN T. & G.

Lassetter (1972, 1975, 1978, 1984) has shown that the three *Vicia* taxa formerly treated as separate species (Hermann 1960) — *V. exigua* Nutt. in T. & G. , *V. leavenworthii* T. & G., and *V. ludoviciana* T. & G. — are morphologically confluent and most likely part of one evolving species complex: *V. ludoviciana* T. & G. Lassetter (1984) described two subspecies: subsp. *ludoviciana* and subsp. *leavenworthii* (T. & G.) Lassetter

TABLE 2. A KEY TO AND DESCRIPTIONS OF THE VARIETIES OF *LATHYRUS LANSZWERTII* KELLOGG S. L.

Variety	Race [*1]	Plant height (dm)	Plant habit	Rachis length (cm)	Tendrils	Number of leaflets	Leaflet shape	Leaflet length (mm)
1. Tendrils of upper leaves well developed, usually branched, prehensile, stems usually greater than 3 dm long, clambering								
2. Leaflets 8–10, corolla pink to purple, plants of central Washington and Oregon and eastern California east to central Utah								
lanszwertii [*2]		4–8	sprawling or climbing	2–8	long, branched, prehensil	8–10	lanceloate (linear)	20–70
2. Leaflets 6–8, corolla white, plants of central Utah and western Colorado								
pallescens [*4]		2–6	erect to sprawling	3–6	long, branched, prehensil	6–8	lanceolate	20–50
1. Tendrils of upper leaves reduced to simple bristles less than 1 cm long, stems often less than 3 dm long, erect.								
3. Leaflets 2–4, plants of eastern Wash. and adjacent Idaho								
sandbergii [*6]	*bijugatus*	2–4	erect	0.5–2.0	aristate	2–(4)	ovate	25–50
sandbergii [*6]	*sandbergii*	2–4	erect	0.5–2.0	aristate	2–(4)	linear	30–90
3. Leaflets 4–6; plants of central Washington south to Arizona and New Mexico								
4. Flowers 8–10 mm long, racemes from distal internodes on stems; plants of eastern flanks of the Cascade								
aridus [*3]		1–3	erect	2–4	aristate	4–6(8)	linear	20–40
4. Flowers 10–15 mm long, racemes from the middle internodes of stems; plants of Utah, Colo., and Ariz.								
leucanthus [*5]	*leucanthus*	1–3	erect	2–3	aristate	4–6	ovate	20–50
leucanthus [*5]	*arizonicus*	1–3	erect	2–3	aristate	4–6	linear	35–70

[*1] Details of racial differences and relationships are given in the text. Description and distribution based on the examination of:
[*2] var. *lanszwertii*: 333 specimens from WS, WTU, BRY, NY, OSC, ORE.
[*3] var. *aridus*: 73 specimens from WS, WTU, NY, OSC, and ORE.
[*4] var. *pallescens*: 100 specimens examined from WS, WTU, NY, OSC, and ORE.
[*5] var. *lucanthus*: 101 specimens examined from WS, WTU, NY, OSC, and ORE.
[*6] var. *sandbergii*: 145 specimens examined from WS, WTU, NY, OSC, and ORE.

& Gunn. Traditionally, taxa within the complex were separated on the basis of inflorescence length, number of flowers, flower length, and, to a certain extent, geographic distribution (Shinners 1948; Turner 1959; Hermann 1960). While taximetric evidence (Lassetter 1972) seems to support these distinctions, Lassetter (1972, 1984) also points out that, although "all taxa [in

TABLE 3. MORPHOLOGICAL VARIATION IN THE *VICIA LUDOVICIANA* NUTT. EX T. & G. COMPLEX. Data from Lassetter (1984).

Variety	Race [*1]	Plant height (dm)	Rachis length (cm)	Number of leaflets	Leaflet length X
1. Leaflets generally 7–10; flowers opening after peduncles and internodes elongate, young fruit not present when flowers first open.					
ludovidiana [*2]	*ludoviciana*	1–20	(2)4–7(10)	(5)8–11(13)	(6)12–16(25)
	texana	12–19	(2)3–5(7)	(7)8–10(13)	(9)13–21(36)
	exigua	2–11	(2)3–6(8)	(4)6–9(12)	(9)14–25(37)
	producta	1–12	(2)3–7	(5)7–9(11)	(7)10–17(39)
	laxifolia	1–8	(2)3–6(8)	(6)7–10(13)	(6)9–17(26)
1. Leaflets often 11–15; flowers opening before peduncles and internodes elongate, often containing young fruits when first open; leaflets often 11–15.					
Levenworthii [*3]	*levenworthii*	1–10	(2)3–5(6)	(7)11–14(17)	(5)10–15(20)
	Louisiana	3–12	6–9(10)	(10)11–13(14)	(13)15–23(25)

[*1] Details of racial differences and relationships are given in the text and in Lassetter (1984). Specimens examination:
[*2] 417 specimens examined from RSA, UNC, ISC, TEX, USCH.
[*3] 130 specimens examined from UNC, ISC, TEX, USCH.

TABLE 2. EXTENDED.

Leaflet width (mm)	Leaflet L/W ratio	Inflorescence length (cm)	Number of flowers	Flower length (mm)	Flower color	Distribution
1. Tendrils of upper leaves well developed, usually branched, prehensile, stems usually greater than 3 dm long, clambering						
2. Leaflets 8–10, corolla pink to purple, plants of central Washington and Oregon and eastern California east to central Utah						
5–20	3–5(10) r	3–9	2–6	10–15	blue /purple, occ. white	central Wash. to Calif. e. to central Utah
2. Leaflets 6–8, corolla white, plants of central Utah and western Colorado						
7–16	2–6 r	5–10	2–4	10–15	white	central Utah
1. Tendrils of upper leaves reduced to simple bristles less than 1 cm long, stems often less than 3 dm long, erect..						
3. Leaflets 2–4, plants of eastern Wash. and adjacent Idaho						
5–15	3–6 r	2–3	2–4	8–10	pink to blue	e. Wash. to Flathead Co., Mont.
2–5	10–30 r	2–3	2–4	8–10	pink to blue	e. Wash. to Flathead Co., Mont.
3. Leaflets 4–6; plants of central Washington south to Arizona and New Mexico						
4. Flowers 8–10 mm long, racemes from distal internodes on stems; plants of eastern flanks of the Cascade						
2–5	8–15 r	2–4	2–4	7–10	white	central Wash. to ne. Calif.
4. Flowers 10–15 mm long, racemes from the middle internodes of stems; plants of Utah, Colo., and Ariz.						
4–15	2–5 r	3–5	2–5	10–15	white	s. Utah, sw. Colo., n. Ariz., nw. New Mexico
2–5	6–35 r	3–5	2–5	10–15	white	s. Utah, sw. Colo., n. Ariz., nw. New Mexico

the *V. ludoviciana* complex] are very efficient selfers", there is the much stronger tendency toward autogamy in populations delimited as subsp. *leavenworthii*: styles and anthers in flowers of subsp. *leavenworthii* are shorter and pollination takes place before the flowers open completely and peduncles are fully elongated. This tendency probably explains why populations of subsp. *leavenworthii*, geographically sympatric with other members of the species complex in Oklahoma and east Texas, have always been recognized, while other morphological variants within the *V. ludoviciana* complex in Texas — *V. texana* T. & G., *V. occidentalis* Shinners, and *V. laxiflora* Shinners — included in *V. ludoviciana sensu* Lassetter (1984) intergrade. Herein I propose varietal names for the subspecies described by Lassetter (1984).

Vicia ludoviciana var. *ludoviciana* includes populations from California (*V. exigua* Nutt. ex T. & G.), populations distributed across the southwest from Arizona and Colorado east to

TABLE 3. EXTENDED.

Leaflet width (mm)	Leaflet L/W ratio	Inflorescence length (cm)	Number of flowers	Flower length (mm)	Distribution
1. Leaflets generally 7–10; flowers opening after peduncles and internodes elongate, young fruit not present when flowers first open.					
(1)2–5(11)	(2)3–5(8)	(2)2–6(11)	(1)4–9(19)	(4)5–7(8)	e. Tex. e. to Alab.
(1)2–4(6)	(2)4–8(15)	(1)3–6(11)	(1)2–6(10)	(4)5–6(7)	s. Tex.
(1)2–3(6)	(4)6–11(16)	(2)3–6(11)	(1)4–9(19)	(4)5–7(8)	S. Calif. to Baja
1–2(4)	(3)6–10(16)	(0)1–4(5)	1–3(5)	(5)6–7(8)	Ariz., sw. Utah, Colo, Okla, w. Tex.
1–4(8)	(2)4–8(10)	(1)3–10(15)	(1)5–15(17)	(5)6–7(9)	e. central Tex.
1. Leaflets often 11–15; flowers opening before peduncles and internodes elongate, often containing young fruits when first open; leaflets often 11–15.					
(1)2–4(6)	(2)3–5(7)	(1)3–6(9)	(1)2–4(6)	(4)5–7(8)	e. Tex., Okla.
(4)6–9(11)	2–3	3–7(9)	1–2	(4)5–7(8)	Ark. Louis.

TABLE 4. MORPHOLOGICAL VARIATION IN *VICIA NIGRACANS* HOOKER & ARNOTT SENSU LATO. Data from Lassetter and Gunn (1979) and collections in OSC, ORE, and WILLU.

Variety	Plant height (dm)	Stipule lengh (mm)	Stipule width (mm)	Rachis length (cm)	Number of leaflets	Number of flowers	Flower length (mm)	Calyx length	Pod length (mm)	Pod width (mm)	Distribution
1. Stems generally > 20 dm in length, leaflets 6–14 in number.											
nigricans	20–30	up to 14	up to 7	5–23	6–14(18)	4–25	13–24	1/4–1/3 of corolla	37–46	8–10	montane central Chile
1. Stems generally < 20 dm in length, leaflets > 14 in number.											
gigantea	6–20	up to 25	up to 15	9–23	16–29	6–19	10–15	1/2 of corolla	33–55	10–20	coastal: san Luis Obispo Co. Calif. to Sitka, Alaska

central and west Texas (*V. producta* Rydb.), as well as the populations found from central Texas east into Louisiana (*V. ludoviciana s.s.*). Lassetter (1984) has described five morphological races within *V. ludoviciana* var. *ludoviciana*; differences among these races are summarized in Table 3. The distribution of these taxa is well documented in Lassetter (1984).

Vicia ludoviciana Nutt. ex T. & G. var. **leavenworthii** (T. & G.) Broich comb. nov. *Vicia leavenworthii* T. & G. Fl. N. Amer. 1:271. 1838. *Vicia leavenworthii* var. *typica* Shinners. Field and Lab. 16:22. 1948. *Vicia ludoviciana* subsp. *leavenworthii* (T. & G.) Lassetter & Gunn, USDA Tech. Bull. No. 1601:16. 1979. Type: USA; Arkansas, [Co. unknown], *Dr. Leavenworth s.n.* (holotype NY!). *Cracca erotanthos* Alefeld. Bonplandia 9:118. 1861. Type: *Hale, s.n.* [sent to Alefeld by Dr. Hexamer of New York], (location unknown).

Vicia ludoviciana var. *leavenworthii* includes two races: one form confined mostly to central and eastern Texas, the other, a robust race with large ovate leaflets and only 1–2 cleistogamous flowers per raceme, found in Arkansas, Louisiana and Mississippi (Table 3).

VICIA NIGRICANS H. & A.

On the basis of morphological similarities, similar habitats, and identical karyotypes, Lassetter and Gunn (1979) have proposed that North American Pacific Coast species *Vicia gigantea* Hook. is conspecific with *V. nigricans* H. & A. of South America and referred to populations of *V. gigantea* as *V. nigricans* subsp. *gigantea* (Hook.) Lassetter & Gunn. Isely (1998) retains the name *Vicia gigantea* Hook. at the specific level. Herein I propose the new combination *V. nigricans* H. & A. var. *gigantea* (Hook.) Broich.

Vicia nigricans var. *nigricans* generally has longer stems, fewer leaflets, and larger flowers (Table 4). It is found in the mountains of central Chile and extreme western Argentina and is usually associated with the austral *Nothofagus* forest (Lassetter and Gunn 1979). *Vicia nigricans* var. *gigantea* is mostly restricted to coastal areas of North America from San Luis Obispo Co., California, to Sitka, Alaska. Variety *gigantea* also occurs inland along the Columbia River and in the Willamette Valley to the foothills of the Cascades in western Oregon.

Vicia nigricans H. & A. var. **gigantea** (Hook.) Broich comb. nov. *Vicia gigantea* Hook., Fl. Bor. Am. 1:157. 1831. *Vicia nigricans* subsp. *gigantea* (Hooker) Lassetter & Gunn, Pacific Science 33:97. 1979. Type: in open wood, common Northwest America, *Douglas s.n.* (K).

Vicia sitchensis Bong., Mem. Acad. Sci. St. Peters., ser. 6, 129–130. 1833. Type: no specimen cited, no known lectotype designated.

Vicia hookeriana Walpers, Rep. Bot. Sys. 1:715–716. 1842. Type: no specimen cited, no known lectotype designated.

Lathyrus cinctus S. Wats., Proc. Amer. Acad. Arts Sci. 23:263. 1889. Type: "Jolon", Monterey Co., *T. Brandegee in 1886* (GH)

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A NEW COMBINATION AND NEW CHROMOSOME COUNTS IN THE TARWEED TRIBE (COMPOSITAE–MADIEAE)

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ABSTRACT

A new combination, **Deinandra peninsularis** (Moran) B. G. Baldwin, comb. nov., is proposed for *D. greeneana* subsp. *peninsularis* of Baja California, Mexico, a taxon that does not belong within *D. greeneana*, based on recent molecular and cytogenetic work. New chromosome counts for *D. peninsularis* and *D. streetsii* and previously reported counts for the other 20 species of *Deinandra* indicate that all perennial or facultatively perennial taxa of the genus share the modal, and probably basal, chromosome number of $2n = 12_{II}$. A new chromosome count for another member of the tarweed tribe, *Arnica mallotopus* [≡ *Mallotopus japonicus*] ($2n = 19_{II}$), in Arnicinae, strongly contrasts with an earlier (somatic) count for that species ($2n = 18$), which is often treated in a different genus based in part on the previously reported chromosome number.

Key Words: *Arnica*, Asteraceae, Baja California, chromosome counts, *Deinandra*, Guadalupe Island, Madiinae, tarweeds.

Recent molecular phylogenetic and cytogenetic studies of *Deinandra* Greene sensu Baldwin (1999) [= *Hemizonia* DC. sect. *Madiomeris* sensu Tanowitz (1982) plus "Fruticosae" or "Zonamra" (Clausen 1951; Keck 1959)] indicate that *D. greeneana* (Rose) B. G. Baldwin subsp. *greeneana*, of Guadalupe Island (Baja California, Mexico), is more closely related to the other two Guadalupe Island endemics in *Deinandra*, *D. frutescens* (A. Gray) B. G. Baldwin and *D. palmeri* (Rose) B. G. Baldwin, than to *D. greeneana* subsp. *peninsularis* (Moran) B. G. Baldwin, from peninsular Baja California and the Todos Santos Islands, near Ensenada (Baldwin 2007). Based on those molecular and chromosomal findings, *D. greeneana* subsp. *peninsularis* does not belong within *D. greeneana* or any other described species of *Deinandra* and warrants taxonomic recognition at species rank.

Deinandra peninsularis (Moran) B. G. Baldwin, comb. nov. Basionym: *Hemizonia greeneana* subsp. *peninsularis* Moran, Transactions of the San Diego Society of Natural History 15:286. 1969. *Hemizonia greeneana* var. *peninsularis* (Moran) B. L. Turner. *Deinandra greeneana* subsp. *peninsularis* (Moran) B. G. Baldwin. Type: Mexico, Baja California, Punta Banda, summit of Banda Peak, *Moran 13437* (holotype, SD; isotypes, K, MEXU, UC, US, etc.).

As noted by Moran (1969), plants treated here as *Deinandra peninsularis* generally differ in habitat, growth form, and leaf, pappus, and fruit characters from the shrubby *D. greeneana* of Guadalupe Island. Artificial hybrids between another shrubby species from Guadalupe Island, *D. frutescens*, and *D. peninsularis*, which have been regarded as conspecific (as *D. frutescens*, e.g., Wiggins 1980; see Moran 1969), were of reduced fertility compared to hybrids between *D. frutescens* and either of the other two Guadalupe Island species (Baldwin 2007).

New chromosome counts were obtained, using the methods of Baldwin (1992), from *D. peninsularis* and other members of tribe Madieae sensu Baldwin (see Baldwin et al. 2002), in subtribes Arnicinae and Madiinae, for which chromosome numbers either have not been published or are at variance with the counts reported here, as indicated below. All counts were obtained from plants grown under greenhouse or growth-chamber conditions from wild-collected seed (for *Deinandra*) or from rhizomes obtained from the Tohoku University Botanical Garden, Japan (for *Arnica mallotopus*).

Deinandra peninsularis (Moran) B. G. Baldwin, $2n = 12_{II}$, Mexico, Baja California, Punta Banda, northwest of La Bufadora, N31°44′ W116°43′, *J. P. Rebman 6037* (SD).

Deinandra streetsii A. Gray, $2n = 12_{II}$, Mexico, Baja California, West San Benito Island (just s. of lighthouse), N28°18′ W115°35′, *S. Junak 5332* (SBBG).

With the addition of these new counts, all perennial or facultatively perennial taxa in *Deinandra* have been reported to have $2n = 12_{II}$, which is modal in the genus (Carr 2003) and may be the base chromosome number for *Deinandra* (Baldwin 2007).

Arnica mallotopus (Franch. & Sav.) Makino [= *Mallotopus japonicus* Franch. & Sav.], $2n = 19_{II}$, Japan, Honshu, Prefecture Yamagata, Mt. Iide, *T. Kikuchi s.n.* (TUSG 6126).

The previously reported somatic count of $2n = 18$ for *A. mallotopus* by Matsuura and Sutô (1935) does not appear to be the result of miscommunication of a meiotic number, based on their accompanying camera-lucida drawing, which shows 18 mitotic chromosomes. That earlier count and the unusual capitulescence morphology of this endemic Japanese species, with densely white-villous peduncles and cylindrical, discoid heads, have contributed to uncertainty about its relationships, as reflected by treatment of these plants within the monotypic genus *Mallotopus* Franch. & Sav. by some botanists. The count reported here is consistent with results of molecular phylogenetic data (Baldwin and Wessa 2000; Baldwin et al. 2002), which placed *A. mallotopus* well within the circumboreal (primarily North American) genus *Arnica* ($x = 19$).

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A NEW HYBRID CHERRY, *PRUNUS* ×*PUGETENSIS* (*P. AVIUM* × *EMARGINATA*, ROSACEAE), FROM THE PACIFIC NORTHWEST

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ABSTRACT

A natural hybrid, **Prunus ×pugetensis** A. L. Jacobson & Zika, is described as the cross between introduced *Prunus avium* (L.) L. of Eurasia, and indigenous *P. emarginata* (Douglas ex Hook.) Eaton of western North America. It is intermediate in morphology, differing from *P. avium* in its pubescence, more slender leaves, smaller flowers, and peduncled inflorescences. It can be separated from *P. emarginata* by its broader leaves with coarser teeth, larger flowers with weakly notched petals, and occasional umbellate inflorescences. Unlike the parents, more than 99% of the flowers eventually abort and it rarely produces fruit. Spontaneous hybrids have been found in the lowlands of western British Columbia, Washington, and Oregon.

Lectotypes are selected for *Cerasus californica* Greene, *Cerasus emarginata* Douglas ex Hook., *Cerasus erecta* C. Presl, *Cerasus kelloggiana* Greene, *Cerasus mollis* Douglas ex Hook., and *Prunus corymbulosa* Rydb.

Key Words: hybrid, lectotype, *Prunus avium*, *Prunus ×pugetensis*, *Prunus emarginata*, Puget Sound, Rosaceae.

Prunus is a highly varied genus of widely distributed trees and shrubs, united by floral and fruit characters, and a base chromosome number of $x = 8$ (Bortiri et al. 2001). Estimates of the number of species of *Prunus* sensu lato range from 200+ (Mabberley 1997) to 430 (Huxley et al. 1992). As we view it, the genus consists of almonds, apricots, cherries, peaches, plums, and cherry laurels. Some botanists (e.g., Browicz and Zohary 1996; Lu et al. 2003) divide *Prunus* sensu lato into as many as six genera, restricting the genus *Prunus* exclusively to plums (Endo 2001; Ku and Bartholomew 2003a). In that sense, the cherries become *Cerasus* Mill., *Padus* Mill., and *Laurocerasus* Duhamel (Ohba and Endo 2001; Li and Bartholomew 2003; Ku and Bartholomew 2003b; Lu and Bartholomew 2003). Our view, like that of the majority of taxonomists in North America, is to consider *Prunus* in the broad sense, including *Cerasus* and the other groups as subgenera and sections (Rehder 1940; McVaugh 1951; Mowrey and Werner 1990). This view is supported by the molecular work and conclusions of Lee and Wen (2001), Bortiri et al. (2001), and Rohrer et al. (2004).

Washington state is a major source for commercial sweet cherries, and has plentiful native cherries. In the late 1980s the first author noticed cherry trees whose identification perplexed him. Since the late 1990s we analyzed these wild cherries, and they appeared intermediate between native *Prunus emarginata* (Douglas ex Hook.) Eaton and the widely cultivated and naturalized *P. avium* (L.) L. Careful appraisal of our data suggests they represent a hybrid. The trees are intermediate in morphology; we have done no cytological or molecular analysis. In this paper we provide descriptions, a key, and comparative tables for the hybrid and its parents. We also reviewed the synonyms of *P. emarginata* and inspected all available types to be sure none represented the hybrid between *P. avium* and *P. emarginata*. We found six epithets typified by a series of syntypes and no holotype, so in this paper we designated a lectotype, based on the protologues and the best of the original material available to the authors when the basionym was published, in accordance with the Code (Greuter et al. 2000).

SPECIES TREATMENT

Prunus × pugetensis A. L. Jacobson & Zika hyb. nov. (*Prunus avium* × *P. emarginata*). (Fig. 1).–TYPE: USA, Washington, Snohomish Co., wooded slope 0.3 km W of Blackmans Lake; below SW side of Bickford Ave, 50 m S of Rte 9 bridge, elev. 60 m, 47°55.9'N, 122°6'W, 4 May 2003, *Zika 18302*. (Holotype: WTU; isotypes: CAN, GH, K, MO, NY, OSC, RM, RSA, UBC, UC, US, V, WS).

Arbor inter Prunus avium et Prunus emarginatam verosimiliter ex hybridatione specierum orta, ambae fructibus abortivis differt; differt a P. avio foliis angustioribus et pubescentibus cum dentibus minoribus et plus numerosis, petalis

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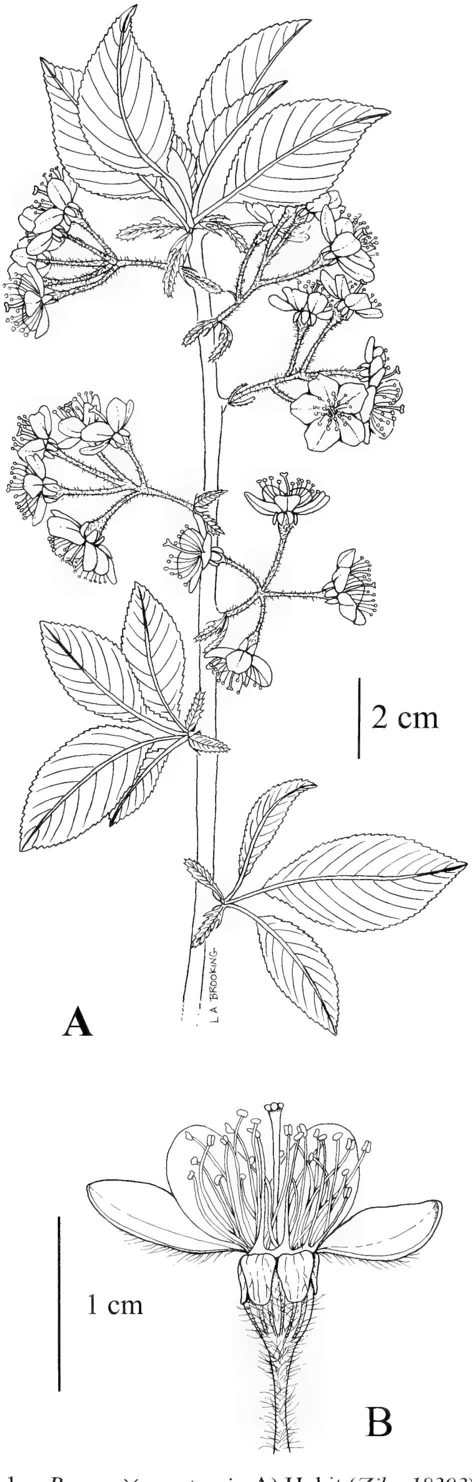

FIG. 1. *Prunus* ×*pugetensis*. A) Habit (*Zika 18303*). B) Flower with one petal removed.

pubescentibus et minoribus, ramunculis pubescentibus, inflorescentiis variantibus ex umbellatis ad pedunculatis vel corymbosis; differt a P. emarginata foliis obovatis longioribus dentatis, petalis 7–14 mm.

Tree, attaining 27 m in height and 48 cm diameter at breast height in the forest, flowering at 3–5 m; solitary or spreading by root sprouts; *bark* usually dark gray to dark coppery-brown, somewhat shiny and smooth, with pale thin corky horizontal lenticels; *twigs* brown, slender, new growth pubescent (rarely glabrous *Zika 19380*); *winter buds* narrowly ovate, several red-brown to dark red-brown scales, proximal scales slightly ciliate-serrate near apex; *leaf scar* crescent-shaped to triangular, with a central elliptical to circular bundle scar, this larger than the two lateral circular bundle scars near distal or lateral margin of leaf scar; *leaves* folded in bud (conduplicate), alternate, thin, elliptic-obovate or narrowly obovate, 4.4–14.7 × 2.1–5.8 cm wide in mid-summer; usually pubescent, mid-green, paler below, serrate, 6–11 teeth per cm in mid-summer, teeth 0.1–1.1 mm high measured from sinus; petiole apex often with 1–2 discoid glands 0.6–1.5 mm diameter; stipules 4–8 mm long, early deciduous, linear to narrowly lanceolate, pectinate to deeply lacerate; leaves deciduous in late October, when turning soft pastel shades of yellow, orange, reddish, or occasionally purple; *inflorescence* axillary, variable, an umbel, peduncled umbel, or corymb, 2–9 flowers per inflorescence, pubescent; rachis 0–1.4 cm; peduncle 0–31 mm long; peduncle uncommonly bearing 1–2 leafy bracts 10–26 × 4–10 mm wide, bracts crenate or serrate with shallow teeth 0.4–0.5 mm high; *flowers* white, rotate, 13–28 mm diameter (fresh), hypanthium campanulate, pubescent, *petals* 5, suborbicular or squarish, varying to ovate, elliptic, or broadly elliptic-oblong, 6.8–14 mm long, entire to slightly notched, base glabrous to lightly pubescent with long crinkled hairs on inner surface, outer surface thinly hairy; *sepals* green, entire, reflexed in flower, 2.4–3.2 mm long, margins ciliate or glabrous, outer surface glabrous (*Zika 19380*) or more commonly lightly pubescent, broadest at base, lance-oblong; *stamens* 20–38; anthers yellow, broadly elliptic, 0.5 mm long (dried); filaments white, filiform, 3–10 mm long, inserted in 2–3 loose series at or near apex of hypanthium, *ovary* glabrous, ovate, 2 ovules (only one maturing), stigma a flattened irregular disk 0.6–0.7 mm wide; style filiform, 0.8–0.9 mm long, slightly broadened at base and at apex; most ovaries aborting; *pedicel* in flower 5–35 mm long, pubescent and often glandular, often subtended by slender quickly deciduous stipule-like pale bracts; fruiting receptacle a disk 1.5–2.2 mm wide; *fruit* subglobose to broadly elliptic-globose, recessed at pedicel attachment; green when immature, ripening to yellow, brownish yellow, or red, with yellow to red blush, with a darker longitudinal line on one side, fruit 10–17 × 9–19 mm wide, slightly shiny, glabrous, flesh 3–4 mm thick, juicy, slightly bitter and slightly sour; *seed* elliptic-globose, slightly flattened, pale

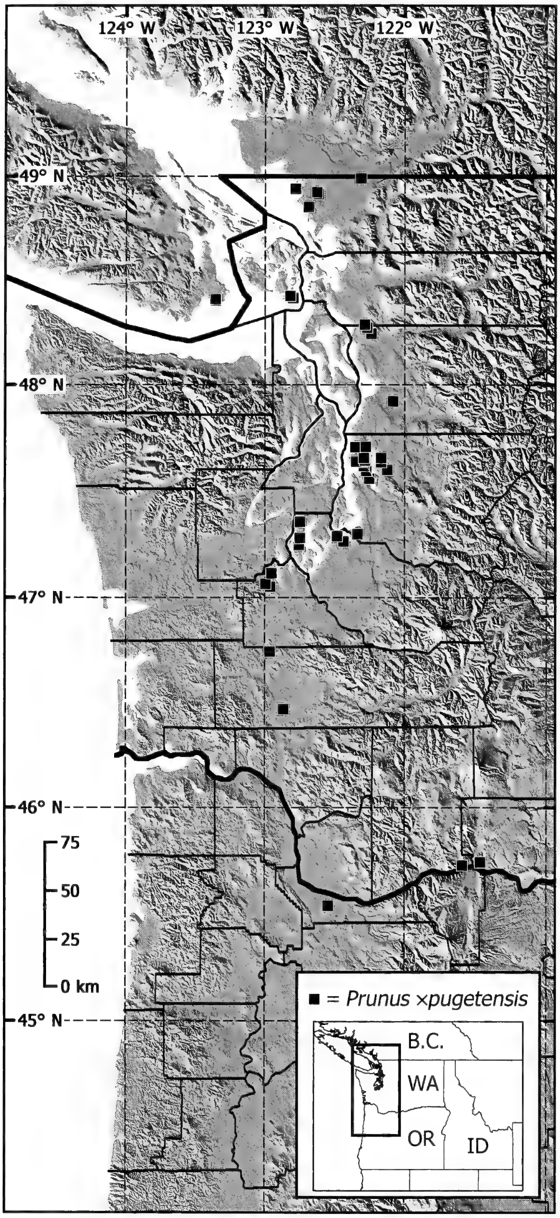

FIG. 2. Distribution of *Prunus* ×*pugetensis*.

brown, 7–11.1 × 5.0–7.8 mm wide, with 5 strong grouped and raised longitudinal ridges, as well as 2–4 small straight unbranched lateral raised veins. Chromosome number unknown.

Distribution. Known populations of the hybrid extend from Portland, Oregon, north to Victoria, Vancouver Island, in southwestern British Columbia, and include the islands of northern Puget Sound (Fig. 2). All known populations are from low elevations west of the Cascade Mountains, and in the Columbia River Gorge. This is entirely within the overlap of native populations of *Prunus emarginata* and naturalized *P. avium*. To commemorate the type locality and its presently known center of distribution, we propose an epithet for Puget Sound.

Paratypes. CANADA, BRITISH COLUMBIA: Vancouver Is., Victoria, Beacon Hill, E slope near summit, elev. 40 m, 6 May 2002; *Zika 16848 et al.* (UVIC, V, UBC, DAO, CAN, TRT, WTU); Vancouver Is., Victoria, Beacon Hill, near Michigan Street, elev. 15 m, 6 May 2002, *Zika 16846 et al.* (UC, K, NY, MT, CAN, DAO, UBC, V, UVIC, UWO).

USA, OREGON: Multnomah Co., Portland, junction of Routes I-84 and I-205, elev. 100 m, 12 Apr 2004, *Zika 19358* (OSC, WTU).

WASHINGTON: King Co., Seattle, Montlake, near SW shore of Portage Bay, elev. 15 m, 20 Jun 2001, *Zika 16311 & Jacobson* (WTU); King Co., Seattle, Montlake, near Oceanography complex, elev. 20 m, 23 Apr 2004, *Zika 19412* (RSA, WTU); King Co., Seattle, Columbia, junction of S Oregon Street and 50th Avenue S, elev. 15 m, 13 May 2005, *Jacobson & Zika 20552* (WTU); King Co., Seattle, Queen Anne, Mt. Pleasant Cemetery, elev. 90 m, 13 May 2005, *Jacobson & Zika 20551* (WTU); King Co., Seattle, Carkeek Park, N of Pipers Creek, elev. 45 m, 13 May 2005, *Jacobson & Zika 20550* (WTU); King Co., Seattle, Capitol Hill, E Mercer Street, elev. 115 m, 20 Apr 2001, *Zika 15950 & Jacobson* (WTU); King Co., Seattle, Leschi, Mt. Baker Ridge, Frink Park, elev. 30 m, 20 Apr 2001, *Zika 15951 & Jacobson* (WTU); King Co., Seattle, Lake City, Thornton Creek floodplain, elev. 35 m, 21 May 2002, *Zika 16910 et al.* (WTU); King Co., Seattle, campus of University of Washington, near 45th Street, elev. 75 m, 26 Oct 2002, *Zika 18141 & Jacobson* (WTU); King Co., Bellevue, W shore of Larsen Lake, elev. 80 m, 20 Apr 2001, *Zika 15946 & Jacobson* (WTU); King Co., Bellevue, Route I-405, 11 May 2003, *Zika 18333* (K, PRA, WTU); King Co., Kirkland, Route I-405, 11 May 2003, *Zika 18334* (WTU); King Co., Redmond, SW side of Grass Lawn Park, elev. 95 m, 17 May 2006, *Zika 22736* GH; King Co., Federal Way, Saghalie Playfield, elev. 100 m, 14 May 2002, *Zika 16869* (CAN, GH, K, MO, NY, UC, US); Klickitat Co., White Salmon, 3 air km S of McCoy Flat, elev. 260 m, 13 Apr 2004, *Zika 19380* (OSC, UC, WTU); Lewis Co., Centralia, Fords Prairie, Route I-5, elev. 60 m, 5 May 2003, *Zika 18308* (WTU); Lewis Co., Drews Prairie, Camas Road, elev. 100 m, 5 May 2003, *Zika 18310* (WTU); Pierce Co., 1.6 km N of Vaughn, Lacey Road, elev. 35 m, 5 May 2003, *Zika 18307* (WTU); Pierce Co., Key Peninsula, 1 km SE of Jackson Lake, elev. 85 m, 5 May 2003, *Zika 18303* (WTU); Pierce Co., Key Peninsula, 1 km W of Bay Lake, elev. 65 m, 5 May 2003, *Zika 18304* WTU; Pierce Co., Tacoma, corner of Tacoma Avenue and N 3rd

Street, elev. 80 m, 28 Apr 2002, *Zika 16819* (WTU); Pierce Co., Tacoma, 45th Street near Verde Street, elev. 80 m, 8 May 2002, *Zika 16851* (OSC, WWB); San Juan Co., Puget Sound, Lopez Is., Point Colville, elev. 15 m, 19 Apr 1996, *Naas 5746 & Arnot* (WTU); San Juan Co., Lopez Is., Watmough Head Road, elev. 30 m, 12 May 2003, *Zika 18341* (CAN, DAO, OSC, UBC, UC, V, WS); Skagit Co., 0.4 air km W of Interstate 5 on Route 20, elev. 10 m, 28 Apr 2006, *Legler 3307* (OSC, WTU); Skagit Co., Padilla Bay National Estuarine Research Reserve, near Interpretive Center, elev. 20 m, 5 May 2006, *Giblin 355* (OSC, WTU); Skamania Co., 3 air km SW of Underwood Mountain, elev. 410 m, 13 Apr 2004, *Zika 19376* (UBC, WS); Snohomish Co., 6 air km SW of Lake McMurray, elev. 95 m, 16 May 2002, *Zika 16877* (GH, MO, NY, OSC, UC, WS); Snohomish Co., 4.5 air km WSW of Lake McMurray, elev. 90 m, 16 May 2002, *Zika 16878* (CAN, DAO, MO, OSC, UBC, V); Snohomish Co., 2.5 air km N of Sunday Lake, elev. 105 m, 16 May 2002, *Zika 16882* (CAS, RSA, UC, WS); Thurston Co., Frye Cove County Park, 3 May 2000, *Wallding 29* ("evsc"); Thurston Co., Brenner Road near Simmons Road, elev. 10 m, 21 Apr 2004, *Zika 19404* (WTU); Thurston Co., 1.5 air km SW of Grass Lake, elev. 20 m, 21 Apr 2004, *Zika 19403* (DAO, RSA); Whatcom Co., 2.3 air km SW of Blaine, 28 Apr 2004, *Legler 1476* (OSC, WTU); Whatcom Co., SW shore of Lake Terrill, elev. 75 m, 28 Apr 2004, *Legler 1478* (WTU); Whatcom Co., 6 km W of Willey Lake, elev. 20 m, 24 May 2002, *Zika 16916* (GH, K, MICH, NY, OSC, RM, US, V, WS); Whatcom Co., 7 km E of Birch Bay, elev. 30 m, 24 May 2002, *Zika 16922* (CAS, ID, MO, MONTU, NY, PRA, RSA, SD, TRT, UWO); Whatcom Co., Halverstick Road, elev. 40 m, 26 Apr 2004, *Zika 19437* (WTU).

Parentage

Prunus avium (L.) L., Flora Suecica, edition 2. 165. 1755.–*Prunus cerasus* L. var. *avium* L., Species Plantarum 1: 474. 1753. TYPE: 22 avium A (holotype: LINN, see Savage 1945).–*Cerasus avium* (L.) Moench, Methodus Plantas Horti Botanici et Agri Marburgensis 672. 1794. 2n = 16, 24, or 32 (Fogle 1975; Montgomery et al. 1997).

Prunus avium is common and fully naturalized in North America, wild in at least 30 states and five Canadian Provinces (Kartesz 2003), where it has been cultivated since about 1600. Its seedlings are a frequent rootstock used for grafting of various fruiting and flowering cherry trees; it rarely sends up root suckers except in woodland settings. Sweet cherry, or mazzard, is also grown purely as an ornamental tree.

In western Washington the flowers first appear in mid-March to April, well before *P. emarginata*, but the flowering period is long and the two overlap. The fruit ripens in early summer, at maturity variously red, purple, inky black, or rarely yellow, a color more typical of some cultivars. Yellow fruits are found in some hybrids, and never in *P. emarginata*. Autumn leaf color for *P. avium* is usually yellow (like *P. emarginata*), but can be a rainbow of green, yellow, orange and red, the same colors that can appear in the hybrid.

Prunus avium is immensely stronger, larger, and longer lived than *P. emarginata* and every other related species cultivated here except *P. serotina* Ehrh. It thrives both in the open and in forests. Woodland specimens can surpass 30 m tall; a stout open-grown tree can reach 17 m tall, its trunk 1 m in diameter, its crown 18.5 m across.

Prunus emarginata (Douglas ex Hook.) Eaton, Manual of Botany for North America, seventh edition. 463. 1836.–*Cerasus emarginata* Douglas ex Hook., Flora Boreali-Americana 1: 169. 1832. TYPE: USA, [Washington, Skamania Co.], common on the outskirts of woods near the Grand Rapids, [Columbia River, elev. 25 m, 45°40'N, 121°54'W; between 31 May and 3 June 1825], *D. Douglas s.n.* (lectotype, here designated, K-351910!).–*Prunus emarginata* (Douglas ex Hook.) D. Dietr., Synopsis Plantarum 3: 42. 1842.–*Prunus emarginata* (Douglas ex Hook.) Walp., Repertorium Botanices Systematicae 2: 9. 1843.

Cerasus mollis Douglas ex Hook., Flora Boreali-Americana 1: 169. 1832. TYPE: On the subalpine hills near the sources of the Columbia [River] and at its confluence [between 1825–1827], *D. Douglas s.n.* (lectotype, here designated, K-351908!, three twigs on the left side of the mixed sheet). – *Prunus mollis* (Douglas ex Hook.) Eaton, Manual of Botany for North America, Seventh Edition: 463. 1836. (Not *Prunus mollis* Torr., Flora of the Northern and Middle Sections of the United States 1: 470. 1824.)–*Prunus mollis* (Douglas ex Hook.) Walp., Repertorium Botanices Systematicae 2: 9. 1843.–*Prunus emarginata* (Douglas ex Hook.) Eaton var. *mollis* (Douglas ex Hook.) Brewer, Geological Survey of California, Botany 1: 167. 1876.–*Prunus emarginata* (Douglas ex Hook.) Eaton var. *villosa* Sudw., United States Department of Agriculture Division of Forestry Bulletin 14: 240. 1897.–*Prunus pensylvanica* L. f. var. *mollis* (Douglas ex Hook.) B. Boivin, Le Naturaliste Canadien 93: 435. 1966.–*Prunus emarginata* (Douglas ex Hook.) Eaton subsp. *mollis* E. Murray, Kalmia 12: 23. 1982.

Cerasus erecta C. Presl, Epimeliae Botanicae 194. 1851. TYPE: [Canada, British Columbia,

northwest Vancouver Island] Nutkta Sund [Nootka Sound, 49°36'N, 126°34'W, in 1791], *T. P. X. Haenke s.n.* (lectotype, here designated, PRC!; isolectotypes: PR-612443!, PR-612444!). [The lectotype labels all mention "Mulgrav portum" (USA, Alaska, Yakutat, Port Mulgrave, 59°34'N, 139°47'W), but this is presumably an error for Haenke's Nootka gathering, on labels made after Haenke's death (Skocdopolová and Štěpánek 2002); the species is not otherwise reported from Alaska (Hultén 1968; Viereck and Little 1972).]–*Prunus erecta* (C. Presl) Walp., Annales Botanices Systematicae 3: 854. 1852.–*Prunus emarginata* (Douglas ex Hook.) Eaton subsp. *erecta* (C. Presl) Piper, Flora of the Northwest Coast. 199. 1915.

Cerasus pattoniana Carrière, Revue Horticole 135. 1872. TYPE: fig. 17.

Cerasus glandulosus Kellogg, Proceedings of the California Academy of Sciences 1: 59. 1873. TYPE: USA, [California, El Dorado Co.], Placerville, *A. Kellogg s.n.* (holotype: ? destroyed by fire at CAS). (Not *Prunus glandulosa* Thunb. in Murray, Systema Vegetabilium, edition 14: 463. 1784 (Bartholomew et al. 1997). Not *Cerasus glandulosa* (Thunb. ex Murray) Loisel., Nouveau Duhamel, ou Traité des Arbres et Arbustes que l'on Cultive en France 5: 33. 1812. Not *Prunus glandulosa* Torr. & A. Gray, A Flora of North America 1: 408. 1840.)

Cerasus californica Greene, Flora Franciscana 1: 50. 1891. TYPE: USA, California, Siskiyou Co., near Yreka, 6 Jun 1876, *E. L. Greene 824* (lectotype, here designated, NDG-23772!).

Prunus corymbulosa Rydb., Memoirs of the New York Botanical Garden 1: 226. 1900. TYPE: USA, Montana, Exploration of Montana and Yellowstone Park, Bridger Mountains, alt. 7000 ft, 18 Jun 1897, *P. A. Rydberg & E. A. Bessey 4437* (lectotype, here designated, NY-436475!; isolectotype: NY-436474!).

Cerasus arida Greene, Proceedings of the Biological Society of Washington 18: 57. 1905. TYPE: USA, California, San Bernardino Co., Bear Valley, San Bernardino Mountains and their eastern base, alt. 6500 feet, 25 Jun 1894, *S. B. Parish 3379* (holotype: US!).

Cerasus crenulata Greene, Proceedings of the Biological Society of Washington 18: 56. 1905. TYPE: USA, New Mexico, "Socorro Co.", Mogollon Mountains, on or near the West Fork of the Gila River, alt. 8,000 feet, 23 Aug 1903, *O. B. Metcalfe 587* (holotype: NDG?, n.v.; isotypes: GH!, US!).–*Prunus crenulata* (Greene) Tidestr., Proceedings of the Biological Society of Washington 40: 119. 1927.–*Prunus emarginata* (Douglas ex Hook.) Eaton var. *crenulata* (Greene) Kearney & Peebles, Journal of the Washington Academy of Sciences 29: 481. 1939.

Cerasus kelloggiana Greene, Proceedings of the Biological Society of Washington 18: 58. 1905. TYPE: USA, California, Placer Co., Emigrant Gap, 28 May 1882, [cited in error as 28 June 1882 in protologue, labeled 28 May 1882 by Jones on all sheets seen], *M. E. Jones 2693* (lectotype, here designated, NY-418580!, isolectotypes: A!, CAS!, DS, NY-803929!, POM!, UC(2), US?, n.v.).

Cerasus obliqua Greene, Proceedings of the Biological Society of Washington 18: 59. 1905. TYPE: USA, California, Butte Co., near Oroville, altitude 175 feet, 2 Oct 1896, *H. E. Brown 117* (holotype: US!; isotypes: NY!, RM).

Cerasus obtusata Greene, Proceedings of the Biological Society of Washington 18: 60. 1905. TYPE: USA, Oregon, [Grant Co.], Silvies-Calamity, southeastern Oregon, Aug 1901, *D. Griffiths & E. L. Morris 810* (holotype: US!). (Not *Prunus obtusata* Koehne, Plantae Wilsonianae 1: 66. 1911.).

Cerasus padifolia Greene, Proceedings of the Biological Society of Washington 18: 59. 1905. TYPE: USA, Nevada, Carson City, foothills, altitude 6000 feet, 2 Jun 1897, *M. E. Jones s.n.* (holotype: US!; isotype: CAS!).–*Prunus padifolia* (Greene) A. Nelson, Botanical Gazette 52: 265. 1911.

Cerasus parvifolia Greene, Proceedings of the Biological Society of Washington 18: 59. 1905. TYPE: USA, California, [Siskiyou Co.], S side of Mt. Shasta, Jul 1897, *H. E. Brown s.n.* (holotype: US?, n.v.).

Cerasus prunifolia Greene, Proceedings of the Biological Society of Washington 18: 57. 1905. TYPE: USA, California, Fresno Co., Dinkey Creek, alt. 8000 ft, 25 Jun-15 Jul 1900, *H. M. Hall & H. P. Chandler 385* (holotype: US!; isotype: K!).–*Prunus prunifolia* (Greene) Shafer, North American Trees. 500. 1908.

Cerasus rhamnoides Greene, Proceedings of the Biological Society of Washington 18: 58. 1905. TYPE: USA, California, Amador Co., Mud Springs, elev. 5500 feet, 1893, *G. Hansen 1474* (holotype: US!; isotype: DS!). (Not *Prunus rhamnoides* Koehne, Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie 52: 283. 1915.)

Cerasus trichopetala Greene, Proceedings of the Biological Society of Washington 18: 60. 1905. TYPE: USA, Montana, Columbia Falls, flower 28 May 1894, *R. S. Williams 1005* (holotype: US?, n.v.; isotypes: MONT!, MONTU!(2)).–*Prunus trichopetala* (Greene) Blank., Montana Agricultural College Science Studies, Botany 1: 70. 1905.

The original collections of bitter cherry, *Prunus emarginata*, were gathered by David Douglas between 1825 and 1827 in the upper Columbia River valley, above Fort Vancouver (McKelvey 1955). The epithet *emarginata* is unfortunate.

TABLE 1. REPORTED HYBRIDS INVOLVING *PRUNUS AVIUM* OR *P. EMARGINATA*.

***Prunus avium* hybrids**
Prunus cerasus L. = *Prunus avium* (L.) L. × *P. fruticosa* Miyoshi (Oldén and Nybom 1968; Mowrey and Werner 1990)
Prunus CV 'Colt' = *Prunus avium* × *P. pseudocerasus* Lindl.
Prunus ×*fontanesiana* (Spach) C. K. Schneider = *Prunus avium* × *P. mahaleb* L.
Prunus ×*gondouinii* (Poit. & Turpin) Rehder = *Prunus avium* × *P. cerasus* (Fogle 1975; Mowrey and Werner 1990)
Prunus ×*schmittii* Rehder = *Prunus avium* × *P. canescens* M. Vilm. & Bois
Prunus ×*stacei* Wójcicki = *Prunus avium* × *P. cerasus* × *P. fruticosa*
Prunus ×*zumbra* Rosend. & Butters = *Prunus avium* × *P. pensylvanica* L.f. × *P. pumila* L. var. *besseyi* (L. H. Bailey) Gleason (Fogle 1975)
***Prunus emarginata* hybrids**
Prunus emarginata (Douglas ex Hook.) Eaton × *P. pensylvanica* (Brayshaw 1996, p. 206; Taylor and Taylor 1981).
Prunus ×*pugetensis* A. L. Jacobson & Zika = *Prunus emarginata* × *P. avium*

Hooker (1832), working with Douglas' manuscript and collections after his death, described the leaves as: "*foliis ... apice obtusis saepe emarginatis*," suggesting the obtuse leaf tips are often shallowly notched. After reviewing the foliage of hundreds of herbarium specimens and wild populations, we have concluded the emarginate apex is an atypical condition, and is barely visible on a few leaves of Douglas' material at Kew.

Although overlooked in modern indices and floras, it has been pointed out by Merrill and Reeder (1946) that the first to make the combination *Prunus emarginata* was Amos Eaton, in 1836. Since its description it has been split into many named variations (e.g., Greene 1905), which we do not recognize. The most commonly accepted named form is pubescent, *P. emarginata* var. *mollis* (Douglas ex Hook.) Brewer (Hitchcock and Cronquist 1961). As far as known, the hybrid *P.* ×*pugetensis* involves only pubescent plants. From our review of types and the literature, none of the names referred to synonymy under *P. emarginata* represent the hybrid *P.* ×*pugetensis*.

Prunus emarginata is found from the Queen Charlotte Islands in British Columbia (c. 54° N) south to Arizona (c. 32° N) and southwestern New Mexico. It is recorded in nine states and one Canadian province (Little 1976; Welsh et al. 1987; Kartesz 2003). The range maps in Little (1976) show *Prunus emarginata* is the western counterpart or extension of *P. pensylvanica* L.f. Their ecological roles are as similar as their appearances. Moreover, where their ranges overlap in British Columbia, they are reported to hybridize (Table 1).

We provide a key to separate *Prunus* ×*pugetensis* from its parents and other members of the genus in the Pacific Northwest. Taxa native, naturalized, or casually escaping from cultivation are included. The key is designed for flowering material, but for certain deciduous taxa it may help to search for the previous year's mature leaves and pits on the ground beneath the tree.

KEY TO *PRUNUS* IN BC, WA, AND OR

1. Leaves evergreen. 2
   2. Inflorescence longer than leaves; petioles and inflorescence rachis dark purple; petal venation dendritic . . . . *P. lusitanica* L.
   2′. Inflorescence shorter than leaves; petioles and inflorescence rachis green; petal venation palmate . . . . *P. laurocerasus* L.

1′. Leaves deciduous 3
   3. Ovary pubescent. 4
      4. Ovary with scattered hairs 5
         5. Flowers pink, in umbels; pedicels 25–40 mm long; leaf tips cuspidate and acuminate. . . . . *P. yedoensis* Matsum.
         5′. Flowers white, in corymbs; pedicels 5–19 mm long; leaf tips gradually acute or obtuse . . . . *P. emarginata*
      4′. Ovary densely hairy. 6
         6. Flowers on pedicels 0.5–1.0 cm long; style base glabrous; flowers white; native shrub in western and southern Oregon . . . . *P. subcordata* Benth.
         6′. Flowers essentially sessile; style base long-hairy; flowers white or pink; trees escaped or persisting from cultivation 7
            7. Axillary buds solitary; terminal winter bud absent; apex of bud scales and sepal margins essentially glabrous; leaves about as long as wide . . . . *P. armeniaca* L.
            7′. Axillary buds in clusters of 3; terminal winter bud present; apex of bud scales and sepal margins tomentose; leaves lanceolate, much longer than wide 8
               8. Flowers white (or palest pink); mature leaves 7–10 cm long, fruit the familiar almond, elliptic, dry, dehiscent, with a thick leathery skin, stone pitted. . .*P. dulcis* (Mill.) D. A. Webb

8′. Flowers pink; mature leaves 10–18 cm long; fruit the familiar peach, subglobose, fleshy, indehiscent, with a thin skin; stone ridged . . . . *P. persica* (L.) Batsch

3′. Ovary glabrous. 9

9. Leaves bronzy or dark purple; flowers white or pink . . . . *P. cerasifera* Ehrh.

9′. Leaves green; flowers white 10

10. Flowers solitary, sessile or on pedicels < 3 mm, anthers yellow-orange to orange-red . . . . *P. spinosa* L.

10′. Flowers usually 2 or more per node, on easily visible pedicels > 5 mm; anthers yellow 11

11. Flowers in racemes or corymbs (inflorescence with a rachis) 12

12. Flowers in short corymbs of 2–15 flowers 13

13. Some sepals erose or glandular serrate, at least towards apex. . . . . *P. emarginata* × *virginiana*

13′. All sepals entire 14

14. Petals 7–14 mm long . . . . *P.* ×*pugetensis*

14′. Petals 4–6 mm long 15

15. Leaves less than 1.5 × as long as wide; leaf bases cordate to nearly truncate; sepals spreading; petals elliptic or elliptic-lanceolate . . . . *P. mahaleb* L.

15′. Leaves more than 2 × as long as wide; leaf bases tapered, cuneate; sepals reflexed; petals suborbicular. 16

16. Leaf tips rounded to acute; bud scales at base of inflorescence persistent; peduncle sometimes leafy, sometimes elongate; widespread in and west of Rocky Mountains. . . . . *P. emarginata*

16′. Leaf tips gradually acuminate or attenuated (well developed on oldest leafy shoots, or on last year's leaves under the plant); bud scales at base of inflorescence usually early deciduous; peduncle never leafy, often 1–2 mm long; east of Rocky Mountains, in our area restricted to SE BC . . . . *P. pensylvanica* L. f.

12′. Flowers in long racemes of 20+ flowers 17

17. Longer petals 6–9 mm long, usually longer than wide; flowers 14–20 mm diam.; inner surface of hypanthium densely pubescent near ovary; last year's pits (look under tree) sculpted and irregularly ridged . . . . *P. padus* L.

17′. Longer petals 3–5 mm long, suborbicular; flowers 10–12 mm diam.; inner surface of hypanthium glabrous or thinly pubescent near ovary; pit surface essentially smooth 18

18. Leaves dull above, underside glabrous; calyx deciduous from developing fruit; isolated small tree, or thicket-forming shrub; common native throughout . . . . *P. virginiana* L.

18′. Leaves glossy above, underside with band of rusty pubescence along lower midvein; calyx persists at base of developing fruit; solitary tree; rare escape from cultivation in urban areas west of the Cascade Mountains . . . . . . *P. serotina* Ehrh.

11′. Flowers in umbels (inflorescence without a rachis) 19

19. Umbels elevated from twig on a peduncle . . . . *P.* ×*pugetensis*

19′. Umbels sessile on twig 20

20. Sepals smooth-margined 21

21. Flowers 23–35 mm diam.; petals 11–16 mm long, tips notched . . . . *P. avium*

21′. Flowers 9–17 mm diam.; petals 4–7 mm long, tips blunt . . . . go to lead 16

20′. Sepals glandular-serrate or glandular-ciliate 22

22. Leaf tips acuminate to attenuate, marginal teeth acuminate and prominent; rare native on our eastern margin . . . . *P. americanum* Marshall

22′. Leaf tips blunt to acute, marginal teeth obtuse to acute, in most species not prominent; native in SW portion of our range, or widely scattered escapes from cultivation 23

23. Hypanthium, pedicels (and usually twigs) pubescent 24

24. Leaves glaucous below; sepals often obscured by dense pubescence, occasionally glabrous; inflorescence often densely pubescent, occasionally glabrous; leaves usually cordate or rounded at base; native in southern and western Oregon. *P. subcordata*

24′. Leaves pale green, not strongly glaucous below; sepals lightly pubescent or glabrous; inflorescence glabrous or sparsely pubescent; leaves cuneate at base; widespread escape from cultivation throughout . . . . *P. domestica* L.

23′. Hypanthium, pedicels (and usually twigs) glabrous 25

25. Hypanthium length < width; sepals with band of hair across base on inner (adaxial) surface; underside of leaf with dense band of hair along lower midvein, otherwise essentially glabrous; flowering in March or the first week of April . . . . *P. cerasifera*

25′. Hypanthium length ≥ width; sepals glabrous within, or uniformly hairy; underside of leaf quickly glabrous, or hairy over entire surface;

flowering in late April or May 26

26. Sepals 3.2–5.0 mm long; flowering pedicels mostly > 1.5 cm long; leaves folded in bud (conduplicate), quickly glabrous beneath, coarsely serrate; leaf base cuneate; fruit the familiar sour or pie cherry; rare escape from cultivation . . . .*P. cerasus* L.

26′. Sepals 2.3–2.7 mm long; flowering pedicels mostly < 1 cm long; leaves rolled in bud (convolute), hairy beneath, finely serrate; leaf base rounded or subcordate; fruit a small plum; native to southern and western Oregon . . . . *P. subcordata*

Ecology

Prunus ×*pugetensis* has been found in thickets, field and forest margins, roadsides, in disturbed second growth conifers, and in mixed conifer and deciduous forest. Elevations range from 10 to 410 m, and sites vary from flat to gentle slopes at all aspects. Common associates include: *Acer circinatum* Pursh, *A. macrophyllum* Pursh, *Alnus rubra* Bong., *Amelanchier alnifolia* (Nutt.) Nutt. ex M. Roem., *Arbutus menziesii* Pursh, *Cornus nuttallii* Audubon ex Torr. & A. Gray, *Corylus cornuta* Marshall, *Crataegus monogyna* Jacq., *Gaultheria shallon* Pursh, *Holodiscus discolor* (Pursh) Maxim., *Oemleria cerasiformis* (Torr. & A. Gray ex Hook. & Arn.) J. W. Landon, *Polystichum munitum* (Kaulf.) C. Presl, *Populus balsamifera* L., *Prunus avium*, *P. emarginata*, *P. virginiana* L., *Pseudotsuga menziesii* (Mirb.) Franco, *Quercus garryana* Douglas ex Hook., *Rhamnus purshiana* DC., *Rosa gymnocarpa* Nutt., *Rubus armeniacus* Focke, *R. spectabilis* Pursh, *R. ursinus* Cham. & Schltdl., *Salix scouleriana* Barratt ex Hook., *Sorbus aucuparia* L., *Symphoricarpos albus* (L.) S. F. Blake, *Thuja plicata* Donn ex D. Don, *Vaccinium ovatum* Pursh, and *V. parvifolium* Sm.

Pollination and dispersal. We have noted a number of insect species visiting the flowers of *Prunus* ×*pugetensis*, including the introduced honeybee (*Apis mellifera*), some *Bombus*, and ants. Flowering has been recorded from 12 April to 24 May. Fruit can ripen by the beginning of June in exceptional years, but typically matures by 15–24 July. We have not observed animals eating the fruits and dispersing the seed of *P.* ×*pugetensis*. Dispersal of the two parents suggests hybrid seeds are probably bird dispersed. We have seen *P. avium* fruits, similar in size to the fruits of *P.* ×*pugetensis*, eaten by American crows (*Corvus brachyrhynchos*), American robins (*Turdus migratorius*), Steller's jays (*Cyanocitta stelleri*), and European starlings (*Sturnus vulgaris*) in the Pacific Northwest. In eastern Canada cultivated *P. avium* fruits are consumed by four bird species: American robins, common grackles (*Quiscalus quiscula*), Baltimore orioles (*Icterus galbula*), and European starlings (Brown 1974). The authors have observed cedar waxwings (*Bombycilla cedorum*) and American robins swallowing *P. emarginata* fruits in western Washington. While the hybrid cherry may be bird dispersed, it is also possible that fallen fruits and seed are moved by a number of mammals (Martin et al. 1961), including Virginia opossum (*Didelphis virginiana*) and raccoon (*Procyon lotor*).

Evidence for Hybrid Status

By using a combination of leaf and inflorescence characters, we found that *Prunus* ×*pugetensis* differed strongly from most wild and cultivated *Prunus* in our area. *Prunus virginiana*, for example, is indigenous and occasional in the range of *P.* ×*pugetensis*, but has black fruits and elongate racemes, unlike the red-fruited umbels and corymbs of *P.* ×*pugetensis*.

The only morphologically similar species, *P. avium* and *P. emarginata*, were also the only representatives of the genus consistently present at populations of *P.* ×*pugetensis*. Both *Prunus avium* and *P. emarginata* are reported to form other hybrids (Table 1). Morphological evidence places *P.* ×*pugetensis* intermediate between the two proposed parental species with which it grows, strongly suggesting that it is a hybrid (Table 2). Leaf shape, size, and toothing of the hybrid are intermediate, as shown in Fig. 3. Characters of the inflorescence, flowering period, fruit size, stone surface, petal shape, autumn leaf color, and winter twigs are also all intermediate, showing the influence of both *P. emarginata* and *P. avium* (Fig. 4). In general, the hybrid is too robust and large in its leaves and flowers to be called *P. emarginata*. It is too slender and pubescent to be called *P. avium* when in flower. Its blooms make a showier display than *P. emarginata*, rather like *P. avium*.

Many known hybrids have reduced fertility. In 2002, we visited wild populations of *Prunus avium*, *P.* ×*pugetensis*, and *P. emarginata* in King Co., Washington, counted flowers on marked branches, and revisited when green fruits were approaching maturity. *P.* ×*pugetensis* aborted more than 99% of its flowers (Table 2), and we had difficulty finding fruits, seeds, and seedlings to include in its formal description, despite searches over five field seasons. In sharp contrast, the fully fertile parents both produced abundant fruit (<40% abortion) and easily detected seedlings. We opened five seeds of *P.* ×*pugetensis*, and they were filled, but we have not run germination experiments to see if they are viable.

TABLE 2. MORPHOLOGICAL COMPARISON OF WILD *PRUNUS AVIUM*, *P.* ×*PUGETENSIS*, AND *P. EMARGINATA* FROM WEST OF THE CASCADES MOUNTAINS IN WASHINGTON AND BRITISH COLUMBIA.

	P. avium	*P.* ×*pugetensis*	*P. emarginata*
Mid-summer leaves			
Shape	Obovate	elliptic-obovate	Elliptic
Marginal teeth/cm	3–7, spread	6–11, ascend	10–21, incurved
Tooth height (mm)	0.3–3.6	0.1–1.1	0.1–0.3
Apex	cuspidate, acuminate	gradually acute	gradually acute or blunt
Length × width (cm)	7–17.5 × 4–8	4–15 × 2–6	2–7.5 × 1–3.5
Mature leaf hairs	± glabrous	mostly pubescent	pubescent
Twigs			
Pubescence	Glabrous	mostly hairy	mostly hairy
Bundle scars	Spaced	usually spaced	usually clustered
Inflorescence			
Inflorescence types	sessile umbel	umbel, peduncled umbel, or corymb	corymb
Leafy peduncle	Never	occasional	occasional
Flowers/inflorescence	2–5	2–9	5–14
Pedicels (mm)	17–64	5–35	5–19
Flowers (shaded plants have the smaller dimensions)			
Diameter (mm)	23–35	13–28	9–17
% early aborted in 2002 (n= number of flowers)	38 (n=429)	99.3 (n=990)	21 (n=771)
Petal pubescence	Glabrous	usually hairy	usually hairy
Petal apex	deep notch	blunt or slightly notched	blunt
Hypanthium	Glabrous	hairy	usually hairy
Ovary	Glabrous	glabrous	glabrous or slightly hairy
Fruits (shaded plants have the smaller dimensions)			
Diameter (mm)	11–21	10–19	7–12
Color	yellow, red, or black	yellow or red	red
Pit (stone, endocarp)			
Shape	subglobose, ellip.-globose	elliptic-globose	ellipsoid
Surface	Smooth	slightly roughened	roughened
Raised lateral veins	Absent	2–4, straight, unforked, short	2–4, curved, forked, elongate
Pit length × width (mm)	9–12 × 7–9	7–11 × 4–8	6–10 × 4–6

Other hybrids between native and introduced species. In our area, there are few records of native species hybridizing with exotics, and such crosses are generally uncommon to rare in the field. Rosaceous examples we have seen include native *Malus fusca* (Raf.) C. K. Schneid. crossing with *M. domestica* Borkh., producing *M.* ×*dawsoniana* Rehder in the Puget Trough (Dickson et al. 1991; Zika 2004). Love and Feigin (1978) discovered introduced *Crataegus monogyna* hybridizing with native *C. suksdorfii* (Sarg.) Kruschke in the wet prairie remnants of the Willamette Valley of Oregon. *Crataegus monogyna* was also found crossing with native *C. punctata* Jacq. in Ontario (Wells and Phipps 1989). In Kitsap Co., Washington, the authors found one clone of *Rosa nutkana* C. Presl × *R. rugosa* Thunb. (*Zika 14908 & Jacobson* WTU). In Québec introduced *Geum urbanum* hybridizes with two native taxa (Bernard and Gauthier 1986).

Outside the Rosaceae, there are a few spontaneous crosses between native North American taxa and exotics, such as in *Impatiens* (Ornduff 1967), *Juglans* (Sargent 1922), *Lupinus* (Wear 1998), *Populus* (Barnes 1961; Spies and Barnes 1982), *Quercus* (Palmer 1948; Hardin 1975), *Schoenoplectus* (Smith 2002), *Spartina* (Anttila et al. 1998), and *Typha* (Smith 2000).

It is likely that there are other hybrids overlooked in our area, when widespread and abundant ones in *Polygonum* (Zika and Jacobson 2003) and *Tamarix* (Gaskin and Schaal 2002; Gaskin and Shafroth 2005) were only recently detected. There is concern about the invasive nature of some hybrids, which are degrading natural areas in the United States (Ellstrand and Schierenbeck 2000), or threatening rare native taxa via introgression (Levin et al. 1996; Rhymer and Simberloff 1996; Vilà et al. 2000). We do not feel that *Prunus* ×*pugetensis* represents a threat to native plant communities in our area. The native parent is common; the hybrid produces insignificant fruit crops (Table 2). We have not observed hybrid seedlings, so we believe *P.* ×*pugetensis* is

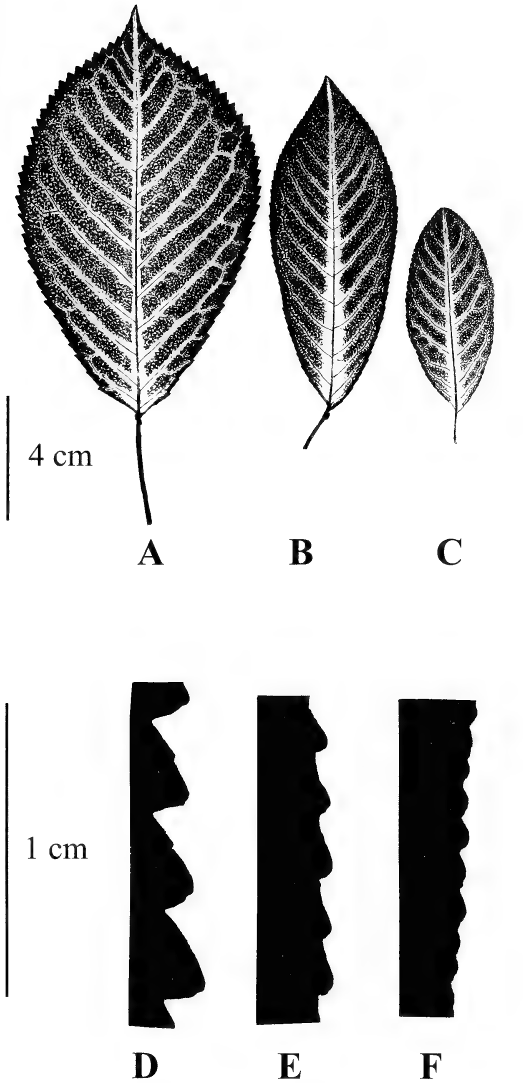

FIG. 3. Comparison of *Prunus* ×*pugetensis* with parents. *Prunus avium* on left, *P.* ×*pugetensis* in center, *P. emarginata* on right. A–C) Leaf shape and size. D–E) Leaf margins.

unlikely to spread aggressively. Each hybrid colony we have found appears to represent essentially sterile spontaneous hybrids, produced locally by crossing of the parental species. Nonetheless, there may be some economic value to the hybrid as an ornamental street tree, with its showy flowers, sturdy growth in urban settings, and lack of fruit. By comparison, the widespread introduction *P. avium* is a much more problematic species in natural areas, with its abundant fruit crop and plentiful reproduction by seed.

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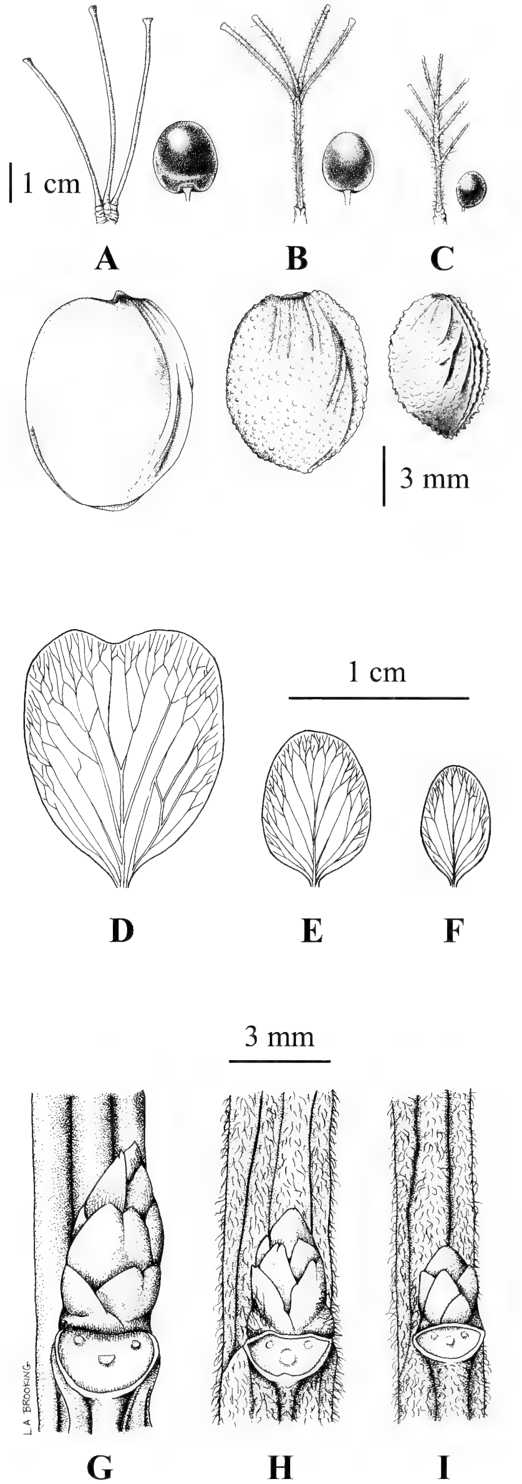

FIG. 4. Comparison of *Prunus* ×*pugetensis* with parents. *Prunus avium* on left, *P.* ×*pugetensis* in center, *P. emarginata* on right. A–C) Inflorescence types, fruit sizes, endocarp surface and size. D–F) Petals. G–I) Winter twigs and buds, leaf scars, vascular bundle scars.

KHD, MICH, MONT, MONTU, NDG, NY, ORE, OSC, POM, PR, PRC, RSA, SD, SOSC, SPC, UBC, US, WILLU, WTU, WTUH, WWB, as well as collections not included in Index Herbariorum (Holmgren et al. 1990): The Evergreen State College, Olympia ("evsc"); Olympic National Forest, Olympia; Olympic National Park, Port Angeles; University of Puget Sound, Tacoma; Pacific Lutheran University, Tacoma; and Reed College, Portland, Oregon. We are grateful to Jan Kirschner and Jan Štěpánek for searching for Haenke collections, to Ken Chambers for correcting the Latin diagnosis, to Ben Legler for preparing the map, to Linda Brooking for Figs. 1 and 4, and to our reviewers for improving the manuscript. Dorothy Naas and Mildred Arnot kindly provided assistance in relocating their station for the hybrid in the San Juan Islands.

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A NEW *PLATANTHERA* (ORCHIDACEAE) FROM YOSEMITE NATIONAL PARK, CALIFORNIA

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ABSTRACT

A new species, **Platanthera yosemitensis** Colwell, Sheviak and P. Moore, from Mariposa County, California, is described and illustrated. Endemic to wet montane meadows between the main stem and the South Fork of the Merced River in Yosemite National Park, it is distinct from *Platanthera stricta* Lindl., *P. sparsiflora* (S. Wats.) Schlecter, and *P. purpurascens* (Rydb.) Sheviak & W. F. Jennings based on vegetative habit, floral morphology, color, and fragrance and pollination mechanics.

Key Words: California, Orchidaceae, *Platanthera*, Sierra Nevada, Yosemite National Park.

The central Sierra Nevada of California supports a small number of *Platanthera* species, including *P. dilatata* (Pursh) Lindl. ex Beck var. *leucostachys* (Lindl.) Luer, *P. sparsiflora* (S. Wats.) Schlechter, *P. stricta* Lindl., and *P. tescamnis* Sheviak & Jennings. *Platanthera purpurascens* (Rydb.) Sheviak & W. F. Jennings was also reported from the central Sierra Nevada of California (Coleman 1995; Sheviak 2002) based on a fragmentary specimen. The range of *P. purpurascens* is otherwise limited to the southern Rockies from southernmost Wyoming to south-central New Mexico and eastern Arizona. The anomalous, disjunct nature of the putative California record stimulated our investigation, which determined that the record was based not on *P. purpurascens* but rather represented an undescribed, endemic species.

DESCRIPTION

Platanthera yosemitensis A. Colwell, C. Sheviak and P. Moore, sp. nov. (Fig. 1). TYPE: USA, California, Mariposa County, Yosemite National Park, northeast of Badger Pass Ski Area, 37°39′N, 119°39′W, 2200 m. Wet meadow with *Platanthera dilatata* var. *leucostachys* Lindley, *Platanthera sparsiflora* (S. Watson) Schltr., *Polygonum bistortoides* Pursh, *Gentianopsis simplex* (A. Gray) Iltis, *Mimulus primuloides* Benth., *Spiranthes romanzoffiana* Cham. Flowers greenish yellow, strongly sweet-spicy-musk scented. 30 July 2003, *A.E.L. Colwell & C. Coulter* 03-33. Holotype: UC 1861834; Isotypes: NYS A33130, YM 117815.

Folia 5–7 prope basin caulis plerumque (suprema infra medium) inserta, supra bracteis redacta. Folium infimum reflexum, ceterum perascendens, 9–25 × 1.5–3 cm. Spica laxe florifera, longitudine 1/2 caulis partes aequantia, aliquantum glauca. Sepalum dorsale viride vel margine flavescenti, porrectum. Sepala lateralia viride reflexa. Corolla citrina. Labellum rhombi-lanceolatum, saepe basi plus minusve rotundati-dilatata, apice plerumque apicem sepalii dorsalis contingenti, interdum libero, labellum tum horizontale, 4–6 mm longum. Calcar saccatum vel scrotiforme inflatum e basi tenui. Columna parvula rotundata, connectivum angustum sed evidens, anthera sacculis parallelis vel aegre divergentibus, lobis rostellii brevissimis prope marginem superiorem orificii calcaris terminantibus. Viscidia orbiculati-quadrata.

Perennial herb, 20–80 cm tall, composed of a single stalk from a horizontal tapered tuberoid and a few fleshy roots, the bud for the subsequent year forming near the base of the current year's stalk on a newly developing tuberoid. Stem stiff and round with minute longitudinal ridges. Leaves 5–7 on the lower 2/5 of stem; Lowest leaf reflexed, ca. 4 cm long × 1 cm wide, the others short-sheathed, clasping, three-nerved, conduplicate, lanceolate, strongly ascending, tapering to an acute, naviculate tip, 9–25 cm long, 1.5–3 cm wide, reduced above to clasping bracts. Inflorescence a lax spike along the upper half of the stem,

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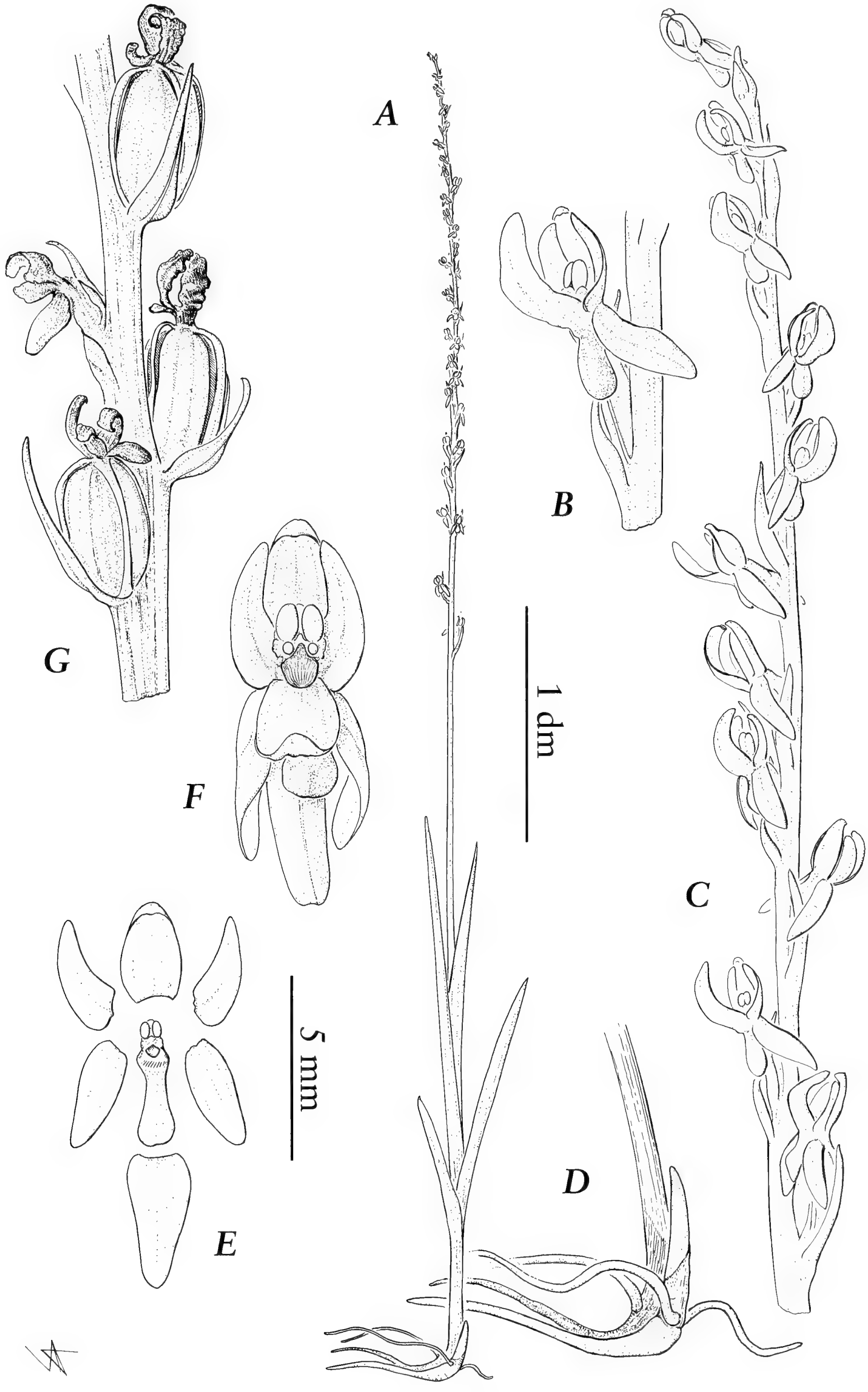

FIG. 1. *Platanthera yosemitensis.* A. Habit; B. Side view of flower; C. Detail of inflorescence; D. Root system; E. Dissected view of flower; F. Front view of flower; G. Detail of mature fruit. Illustration by John Myers.

somewhat glaucous on rachis, floral bracts, and flowers. Flowers 30–50, sparsely arranged in an irregular spiral, floral bracts attenuate, 1-nerved, approximately equaling the ovary. Flowers sessile, resupinate, gradually diminishing in size upwards and the uppermost generally not developing mature fruit. Dorsal sepal green or the margins yellowish, ovate, porrect, partially enclosing and connivent with the petals to form a hood. Lateral sepals green, oblong, slightly tapered to tips, reflexed downwards along the sides of the ovary. Corolla yellow, the segments thick, entire. Petals falcate, obliquely dilated at the base, asymmetrically ovate-deltoid, the upturned obtuse apices approximate, (3–) 4 mm long. Lip rhombic-lanceolate, the base often somewhat rounded-dilated, the apex commonly connivent with the apex of the dorsal sepal, sometimes free and the lip then horizontal but not descending, (4–) 6 mm long. Spur saccate or scrotiform, expanding from a more slender base, (2.0–) 2.8 mm long. Column very small, rounded, the anther erect, connective narrow but evident, anther sacs parallel to slightly diverging, rostellum lobes very short, obscure, the orbicular-quadrate viscidia held above the orifice of the spur. Fruit a stout cylindric capsule, 1 cm long in lowest flowers, diminishing in size upwards to 0.3 cm. Perianth persistent on the capsule apex but shriveling and darkening upon drying.

Chromosome number. $2n = 42$ (*C. Sheviak, A.E.L. Colwell, & A. Sanders* 6998 [NYS A33490], from 3 inflorescences collected at same site as *A.E. L. Colwell & C. Coulter* 03-33).

Flowering period. July–August.

Etymology. This species is named for Yosemite National Park, to which it appears to be endemic (Fig. 2). We suggest the common name Yosemite bog-orchid.

Paratypes. USA, California, Mariposa County: Yosemite near Glacier Point, 14 July 1923, *George Henry Grinnell s.n.* (RSA 382940); Meadow above Chinquapin on road to Glacier Point, 14 July 1923, *George Henry Grinnell* 123 (RSA 382932); Badger Pass, Yosemite National Park, *Mary V. Hood, s.n.* 6 August 1965 (YM 117456); Yosemite National Park, off Glacier Point Road, 14 Jul 1993, *R.A. Coleman s.n.* (NYS A12358); Yosemite National Park, Meadow Brook, 37° 41′N, 119°39′W, 2158 m, 24 July 2003, *A.E.L. Colwell & C. Coulter* 03-22 (YM 117810); Yosemite National Park, Meadow Brook, 37°41′N, 119°39′W, 2158 m, 20 August 2003, *A.E.L. Colwell & C. Coulter* 03-46 (YM 117804); Yosemite National Park, Meadow near Glacier Point Road, 37°39′N, 119°39′W, 2225 m, 13 August 2004, *A.E.L. Colwell & A. Sanders* 04-238 (MO 04479050); Yosemite National Park, Rail Creek, 37°39′N, 119°40′W, 2200 m, 26 September 2004, *A.E.L. Colwell & P. Moore* 04-306 (YM 118100).

Discussion

Distribution and Habitat

Platanthera yosemitensis is currently known from only nine sites within Yosemite National Park, all on the granitic upland south of Yosemite Valley, within 4 km of Monroe Meadows (Fig. 2). As the range is currently known, it is the only orchid species endemic to the Sierra Nevada in California. Its habitat is wet meadows between 2100 and 2285 m elevation in partial shade cast by a surrounding forest of *Abies magnifica* Andr. Murray and *Pinus contorta* Loudon. These meadows are at headwaters of first order streams in steep terrain with forested watershed above them. *Platanthera yosemitensis* occurs within these meadows in sites of active groundwater seepage. Individuals are found in well-developed turf with dense (<1 m tall) herbaceous vegetation, often dominated by *Carex utriculata* Boott, *Dodecatheon alpinum* (A. Gray) E. Greene, *Eleocharis pauciflora* (Light.) Link, *Luzula subcongesta* (S. Watson) Jepson, *Pedicularis attolens* A. Gray, *Perideridia bolanderi* (A. Gray) Nelson & J. F. Macbr., *Phalacroseris bolanderi* A. Gray, *and Polygonum bistortoides.*

The upland area south of Yosemite Valley inhabited by *P. yosemitensis* is noteworthy because it contains several species endemic to the central and southern Sierra Nevada: *Allium yosemitense* Eastw., *Eriophyllum nubigenum* A. Gray, *Hulsea brevifolia* A. Gray, *Ivesia unguiculata* A. Gray, *Senecio clarkianus* A. Gray, *Phalacroseris bolanderi*, and *Trifolium bolanderi* A. Gray. Age and stability of this montane habitat and hence of the composition of the regional species pool (Millar and Woolfenden 1999) is likely a factor related to this level of endemism. This upland remained largely free of ice during the most recent glacial events that scoured much of the Sierra Nevada and carved the valleys to the north and south in the last two million years (Matthes 1930; Alpha et al. 1987). Matthes (1930) infers that, during periods of glacial maxima, this exposed surface was not forested, but was instead covered by an alpine meadow that had seasonal snow cover as the area does currently. The current habitat of *P. yosemitensis* is similar to the habitat described by Matthes and to modern day periglacial environments.

In addition to harboring glacial refugia during the Pleistocene, recent geologic evidence suggests that montane habitat in the Sierra Nevada is significantly older (Small and Anderson 1995; Wernicke et al. 1996; Stock et al. 2004, 2005;

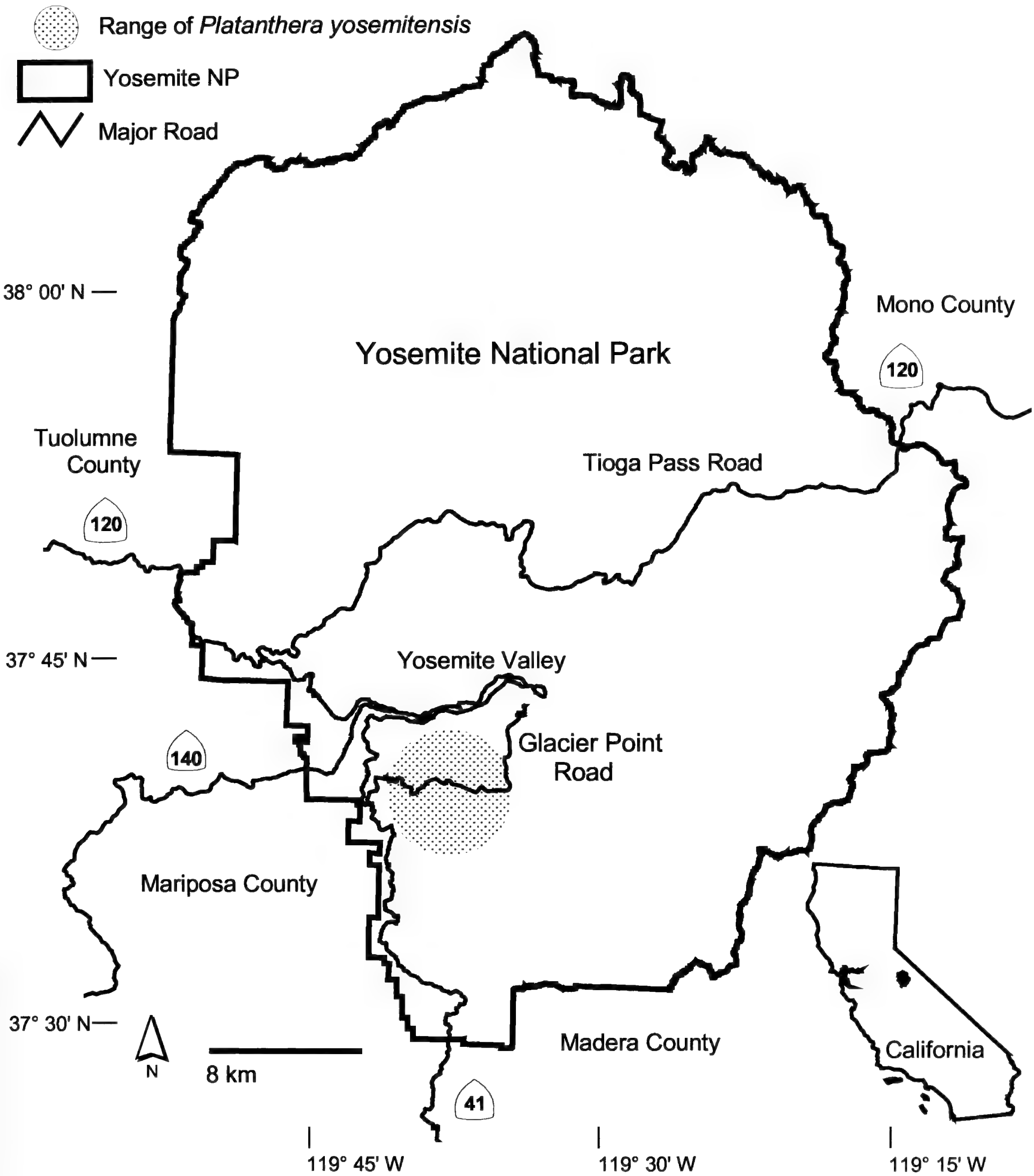

FIG. 2. Range of *P. yosemitensis* in Yosemite National Park, central Sierra Nevada, California.

Mulch et al. 2006), than the few million years previously accepted (Sharsmith 1940; Chabot and Billings 1972; Raven and Axelrod 1978). House et al. (1998, 2001) propose a Cretaceous origin of high elevation mountains in the southern Sierra Nevada. Stock et al. (2005) present evidence that some Sierra Nevada uplands have been eroding very slowly, only about 10 m per million years. Stable montane habitat on the order of tens of millions of years in age should be thought of as a site of in situ speciation of montane plants (Kimball et al. 2004). In this context, the discovery of a distinct orchid species is not surprising and the distribution of *P. yosemitensis* may well be more widespread within this region than is currently known. It should therefore be sought in similarly unglaciated wet meadow sites elsewhere in the central Sierra Nevada.

Taxon Relationships

The *Platanthera* species of the central Sierra Nevada of California include *P. dilatata* var. *leucostachys*, *P. sparsiflora*, *P. stricta*, and *P. tescamnis*. They are part of a transcontinental complex of species long noted for taxonomic intractability. They are not readily determined by superficial examination of gross morphology, but rather require careful study of certain critical characters, especially of the column.

Platanthera sparsiflora has typically been recognized on the basis of a large column filling much of the hood formed by the sepals and petals. More significantly, the viscidia, the sticky pads that affix the pollinaria to the pollinator, are borne on prominent, angular rostellum lobes that present them forward and to either side of, or somewhat below, the orifice of the spur. The connective, the sterile tissue between the anther sacs, is correspondingly very broad. The column is typical of those of *Platanthera* species that place pollinaria on insects' eyes. This configuration is seen in the types of *P. sparsiflora* and its taxonomic synonyms, *Limnorchis laxiflora* Rydb., *Limnorchis ensifolia* Rydb., and *Habenaria aggregata* Howell (See Sheviak & Jennings [2006] for discussion and illustration of types.). The more eastern *P. zothecina* (Higgins & Welsh) Kartesz & Gandhi, of the Colorado Plateau, bears a functionally similar column, but it is not clear if it reflects a common origin or a parallel or convergent development.

In contrast to the broad, angular-lobed column of *P. sparsiflora*, the columns of the other species in the region are small, with abbreviated, more rounded rostellum lobes that present the viscidia closer to the orifice of the spur, typically near the upper margin. Pollinaria are thus placed on the proboscis or mandibles or on the eyes of smaller insects. Among these species, *P. dilatata* var. *leucostachys* is distinguished by its pure white, nocturnally fragrant flowers with slender spurs much longer than the lips. The remaining species bear flowers more or less green or greenish yellow in general aspect. These include the recently described *P. tescamnis* which is discussed at length by Sheviak & Jennings (2006). For purposes of the present discussion, *P. tescamnis* is recognized by a slender to slightly clavate spur somewhat shorter to slightly longer than the lip. The remaining species bear comparatively short, inflated spurs.

Platanthera purpurascens was recently reported from the central Sierra Nevada of California (Coleman 1995; Sheviak 2002) based on a determination by Sheviak of an inflorescence fragment. This species was originally described over a century ago as one of Rydberg's species of *Limnorchis* (Rydberg 1901). Ames (1910) reduced it to varietal status under *Habenaria hyperborea* (L.) R. Br., but subsequently it was largely ignored, even in synonymy, until treated as a variety of *Platanthera hyperborea* (L.) Lindl. by Luer (1975). In the intervening years it had been confused with *P. stricta* Lindl., with which it shares a short, scrotiform or saccate to inflated-clavate spur. This single-character taxonomy is analogous to the recognition of *P. sparsiflora* based on its large column; in both cases, the character reflects a pollination syndrome and is a reliable indicator of neither evolutionary history nor relationship (Sheviak 2002). Of greater significance is the similar vegetative habit of *P. stricta* and *P. purpurascens*. The leaves of both species are relatively short, blunt, commonly widely spaced, and abruptly diverging from the stem, often at nearly 90 degrees. Plants of both species are commonly slender, with long, lax inflorescences, but robust plants can be more densely flowered. However, the two species differ significantly in other details, most significantly in column shape and floral fragrance, and less definitively in flower color and lip shape. In the column of *P. stricta*, the anther sacs and rostellum lobes are approximately parallel or somewhat converging. In contrast, in *P. purpurascens* they are wide-spreading. Flowers of *P. stricta* are scentless or rarely with the faintest hint of a spicy scent; those of *P. purpurascens* are strongly musty scented. These two characters evidently reflect different pollination specializations that would be of species-level significance. Additionally, flowers of *P. stricta* are typically a concolor medium green, with linear oblong lip of the same hue as the rest of the flower. The lip may vary occasionally toward more lanceolate and, in the North, yellowish, but the species is much more uniform than is *P. purpurascens*. In *P. purpurascens*, populations commonly show considerable variation with lip linear lanceolate to broadly rounded-dilated at the base, and varying in color from markedly bluish green to dull yellowish; sometimes it is marked with reddish blotches, hence the specific epithet.

Platanthera yosemitensis differs from *P. stricta* and *P. purpurascens*, the other species with scrotiform-saccate spurs, in vegetative habit. In contrast to the wide spacing and typically abrupt spreading of the rather short, blunt leaves of *P. stricta* and *P. purpurascens*, those of *P. yosemitensis* are long, tapered, ascending, and clustered at the base of the stem. The long, lax inflorescence is then borne on a sparsely-bracted scape.

Flowers of *P. yosemitensis* and *P. purpurascens* show limited similarity. In addition to the spurs, the lanceolate lip, and orbicular to orbicular-quadrate viscidia characteristic of *P. yosemitensis* are typically, if not uniformly, seen also in *P. purpurascens*. A dilation of the base of the lip is common in *P. yosemitensis*, and is sometimes

found in *P. purpurascens*, where it is much less common, but may be more strongly developed. Otherwise, the species differ markedly.

The rachis, floral bracts, pedicillate ovary, and abaxial surfaces of the sepals of *P. yosemitensis* are somewhat glaucous, a condition unique in the genus. Only the very large-flowered *P. zothecina* of the Colorado Plateau is superficially similar in the whitish-green cast of its inflorescence. In that species, however, the whitish coloring is not so much a glaucous bloom as a general pale coloration. Perhaps as a consequence of this glaucous surface, flowers of *P. yosemitensis* persist in a blackened, shriveled state atop the expanded capsules, lending a distinctive aspect to the plant after flowering.

Platanthera yosemitensis is furthermore unique in its concolor rich yellow corolla. In other species with yellowish lips, the hue is more suffused with green or rather dull, and the petals are green or greenish. The clear color throughout the corolla in *P. yosemitensis* is notable. The scrotiform-saccate spur is essentially an extreme development of the inflated-clavate form seen occasionally in *P. stricta* and *P. purpurascens*, pendulously inflated from a short slender base. Whereas saccate spurs in *P. stricta* and *P. purpurascens* are more nearly sessile on the base of the lip, and the more clavate extreme is merely a blunt inflation of a generally tubular structure, in *P. yosemitensis* the nearly spherical sac is born on the summit of a distinct expanding tube.

Platanthera yosemitensis has a pronounced fragrance with a prominent musk component. It has been likened by different observers to a corral of horses, asafœtida, strong cheese, human feet, sweaty clothing, or simply disagreeable. It is similar to the scent of *Polygonum bistortoides*, a frequent component of the meadows *P. yosemitensis* inhabits. Other similar species vary from strongly spicy of cloves (*P. dilatata* vars. *dilatata* and *leucostachys*), sweetly pungent (*P. dilatata* var. *albiflora* (Cham.) Ledeb., *P. huronensis* (Nutt.) Lindl., most *P. tescamnis*, some *P. aquilonis*, etc.), or strongly musty (*P. purpurascens*), to entirely or virtually scentless (*P. stricta*, *P. sparsiflora*; Coleman's report [Coleman 1988] of a sweet scent in the latter was the result of an editing error, [Coleman *pers. com.*]). The combination of scent, the yellow color and the short distance between the viscidia (0.3 mm) in *P. yosemitensis* may be indicative of a mosquito or fly pollination syndrome, which is also reported from the much larger-flowered *P. obtusata* (Raup 1930; Stoutamire 1968; Thien 1969; Gorham 1976).

Platanthera yosemitensis is consistent in vegetative and floral morphology, floral color, and scent, displaying only limited variation. One feature of *P. yosemitensis* is its uniformity of character expression within and between populations. Although its limited distribution might be taken to explain its greatly limited variability, in other *Platanthera*, especially *P. purpurascens*, great variability is commonly seen within even small colonies.

Hybrid formation in *Platanthera* is frequently reported, and is suspected between *P. yosemitensis* and sympatric species. *Platanthera sparsiflora* and *P. dilatata* var. *leucostachys* are common in the same meadows in which *P. yosemitensis* is found. A single plant in each of two *P. yosemitensis* populations appears to have floral characters intermediate between *P. yosemitensis* and *P. sparsiflora*. Phenology provides some measure of isolation as *P. sparsiflora* blooms earlier and is generally in fruit set by the time *P. yosemitensis* plants begin flowering. Furthermore, the different column structures and resulting differences in placement of pollinaria suggest that such crosses must be very rare and are probably the result of exploration by generalist pollinators rather than a properly oriented vector. Similarly, two plants at one site were intermediate in color and morphology between *P. yosemitensis* and *P. dilatata* var. *leucostachys*. Hybridization between these species again would appear to be rare due to the totally incompatible spur lengths. Nonetheless, random visitation by non-adapted insects might more frequently result in hybridization of these species than of *P. yosemitensis* with *P. sparsiflora* because the columns of *P. yosemitensis* and *P. dilatata* are similarly proportioned.

Platanthera dilatata var. *leucostachys* and *P. sparsiflora* often fill all the fruits on their inflorescences. In contrast, *P. yosemitensis* generally matures only the fruits on the lower two-thirds of the inflorescence. A few individuals have been found with all fruits filled, but others, especially those in small populations or on the margin of a population, fill only one or two fruits on an inflorescence. When this is the case, the filled fruits are not necessarily the lowest fruits, or even adjacent to each other on the inflorescence stalk, implying that this species is not self-pollinating.

Conservation Status

All of the known occurrences of *P. yosemitensis* are within the boundaries of Yosemite National Park. It is likely that additional occurrences will be found in the vicinity, especially to the south. Of nine known occurrences, five are located in remote areas, while four are adjacent to areas of frequent human use. The delicate inflorescence of this species is difficult to discern in the dense meadow vegetation in which it grows, which makes *P. yosemitensis* less likely to be noticed or poached. A greater concern is the small number of individuals at most of the sites (at four sites, fewer than ten flowering individuals

TABLE 1. CHARACTERS OF THE CALIFORNIA *PLATANTHERA* SPECIES.

Species	*P. dilatata* var *leucostachys*	*P. sparsiflora*	*P. stricta*	*P. tescamnis*	*P. yosemitensis*
Spur shape	Slender to cylindric	Slender to cylindric	Club-shaped to scrotiform	Clavulate (cylindric)	Scrotiform
Spur length	Greater than 1.5× lip length	Approximately 1× to approximately 1.5× lip length	Approximately 0.25× to less than 1× lip length	0.8 to 1.4× lip length (much less in some scentless plants)	Less than 0.5× lip length
Flower color	White	Green	Green (lip sometimes marked with small areas of fine reddish venation)	Green (lip greenish yellow to yellowish)	Yellow
Scent	Strong spicy	None	None (rarely faintly spicy)	Sweet pungent or none	Strong musk
Viscidia placement	Above spur orifice	Either side of spur orifice	Above spur orifice	Above spur orifice	Above spur orifice
Viscidia shape	Linear to linear-oblong	Orbicular to oblong	Orbicular	Orbicular or oblong	Orbicular-quadrate
Leaf shape	Lance-elliptic to linear elliptic	Lance-elliptic to linear elliptic	Oblong to ovate-lanceolate	Lance-elliptic to linear elliptic	Lance-elliptic to linear elliptic
Leaf orientation	Ascending to gradually arching, internodes obscured	Ascending to gradually arching, internodes obscured or abruptly spreading, internodes exposed	Abruptly spreading, internodes exposed	Ascending to gradually arching, internodes obscured	Ascending to gradually arching, internodes obscured

have been observed), which are at risk of extirpation due to random natural events as well as anthropogenic threats. In order to protect these populations, location details have been left out of the specimens cited above. All of the known sites are in meadows exhibiting encroachment by *Pinus contorta*, a regional phenomenon in the central Sierra Nevada (Millar et al. 2004), which may pose a long-term threat to these populations. Active management may thus eventually be required to insure the species' survival.

The similarity of early season vegetative growth of the three sympatric *Platanthera* species in Yosemite renders surveys for this plant effective only from July to September when the plants are in flower or fruit.

KEY TO THE CALIFORNIA *PLATANTHERA* SPECIES

1. Flower white to cream; spur 1.5× or more the length of the lip, slender, cylindric . . . . *P. dilatata* var. *leucostachys*

1′ Flower green to yellow, spur slightly longer to much shorter than lip; cylindric to variously inflated

  2. Viscidia presented on rostellum lobes to either side of spur orifice; column proportionally large, occupying about 2/3 of the hood formed by the dorsal sepal and petals, the connective very broad, the rostellum lobes prominent, widely spaced, and together with the stigma and connective forming a hemispherical chamber. . . . . *P. sparsiflora*

  2′ Viscidia presented on rostellum lobes above spur orifice; column proportionally small, occupying less than half of the hood formed by the dorsal sepal and petals, the connective narrow, the rostellum lobes scarcely elevated, parallel, diverging, or converging, at most separated by a narrow slit and not forming a hemispherical chamber

    3. Leaves oblong to ovate-lanceolate, widely spaced along stalk, abruptly spreading from base to somewhat ascending, with internodes exposed and clearly evident; spur club-shaped to scrotiform; lip green (sometimes marked with small areas of fine reddish venation); scentless. . . . . *P. stricta*

    3′ Leaves lance-elliptic to linear elliptic, clustered at base of stalk, ascending to gradually arching from base, with long-sheathing leaf bases mostly obscuring internodes; spur slender to scrotiform; lip yellowish; pungent-scented

      4. Spur <0.5 × lip length; saccate to scrotiform; lip bright yellow, inflorescence glaucous; pungent musk scent . . . .*P. yosemitensis*

      4′ Spur 0.8 to 1.4 × lip length; clavulate (-cylindric); lip greenish yellow, inflorescence not glaucous; sweet pungent scent or scentless . . . . *P. tescamnis*

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STREPTANTHUS LONGISILIQUS (BRASSICACEAE), A NEW SPECIES FROM NORTHEASTERN CALIFORNIA

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ABSTRACT

Streptanthus longisiliqus G. Clifton & R. Buck is described as a new species from Butte, Tehama, and Shasta counties in northeastern California. The new species is a short-lived perennial in subgenus *Pleiocardia*, informal group Cordati. Based on several morphological characters, *S. longisiliqus* appears to be most closely related to the montane southern California species *S. bernardinus* and *S. campestris*; it is geographically disjunct from those taxa by approximately 600 km. *Streptanthus longisiliqus* occurs in montane coniferous forest, often in localized openings, and sometimes in disturbed places.

Key Words: Brassicaceae, Butte County, California, new species, *Pleiocardia*, Shasta County, *Streptanthus*, Tehama County.

In 1974, the senior author discovered a *Streptanthus* south of Stirling City in Butte County, California, which could not be satisfactorily identified as any previously described species in the genus. The same taxon was discovered in 1989 at several locations in northern Shasta County in the course of special-status plant surveys along the route of a proposed electric transmission line. A subsequent survey of several herbaria located a number of additional previous collections of this taxon. This *Streptanthus* was first collected by Milo Baker in eastern Shasta County in 1898 (Baker 413 UC). Jepson (1936) cited this specimen as *S. cordatus* Nutt., noting its arcuate fruits, in contrast to the generally straight fruits of *S. cordatus*. A 1967 collection by Arthur Kruckeberg (Kruckeberg 6042 WTU) and several collections by Robert Preston and others at CHSC, collected between 1980 and 1988, documented additional localities in eastern Tehama and eastern Butte counties. The Kruckeberg collection and the collections at CHSC were determined as *S. cordatus* but, like the Baker collection, are substantially different from typical *S. cordatus*. The taxon was noted as an undescribed species in the Butte County flora (Oswald and Ahart 1994) and in the Jepson Manual treatment of Streptanthus (Buck et al. 1993).

In a study of seed glucosinolates in *Streptanthus* species, Rodman et al. (1981) cited the Kruckeberg collection as *S. cordatus* var. *crassifolius*, a name that has apparently never been validly published, based on *Streptanthus crassifolius* Greene. Greene (1897: 227–228) proposed the name *S. crassifolius* to encompass plants from eastern California, Nevada, Arizona, and western Utah that are recognized today as *S. cordatus* var. *cordatus*, restricting *S. cordatus* to plants from Wyoming and eastern Utah. Although Greene did not cite specimens, it is clear that his concept of *S. crassifolius* does not apply to the northeastern California plants herein described as a new species.

The seed glucosinolate profile for Kruckeberg 6042 differed from the profiles determined for other *S. cordatus* accessions (Rodman et al. 1981), which supports our comparative field and herbarium studies that indicate that this northeastern California taxon is not a form of *S. cordatus*. It is more closely related to *S. campestris* S. Watson and *S. bernardinus* Parish, two species occurring in the Transverse and Peninsular Ranges of southern California. Although all three taxa show morphological similarities, the northeastern California taxon, here described as *Streptanthus longisiliqus* sp. nov., consistently differs in several respects from the two southern California species (Table 1). Its southern range limit is approximately 600 km NNW of the northern limits of the two southern California species.

SPECIES TREATMENT

Streptanthus longisiliqus G. Clifton & R. Buck sp. nov. (Fig. 1)—TYPE: USA, California: Butte Co., ±0.8 km north of Robley Point, growing on a steep road bank, 39°52′21″N, 121°31′06″W; T23N R4E S10, NW 1/4 of NW 1/4, 13 June 1997, G. Clifton 35529 (holotype, JEPS; isotypes, CAS, CHSC, PUA, MO, NY, RSA).

Differt a *S. campestris* S. Watson foliis mediis et superis caulinis ovatis vel suborbicularibus, generatim integris, et petiolis foliorum basilarium et infernorum caulinorum generatim glabris.

Short-lived perennial from persistent woody taproot or slender caudex; herbage glabrous, glaucous. Stems 1 to rarely several, erect or ascending, simple or branched above, 3–15 dm

TABLE 1. MORPHOLOGICAL COMPARISON OF *STREPTANTHUS LONGISILIQUS*, *S. CAMPESTRIS*, *S. BERNARDINUS*, AND *S. CORDATUS* VAR. *CORDATUS*. Some data are from Buck et al. (1993).

Character	*S. longisiliqus*	*S. campestris*	*S. bernardinus*	*S. cordatus* var. *cordatus*
Plant height	6–15 dm	3–15 dm	3–6 dm	2–6 dm
Petiole pubescence	Generally glabrous	Generally ciliate	Generally glabrous	Glabrous or ciliate
Middle, upper cauline leaf	Ovate to suborbicular, generally entire	Lanceolate to lance-oblong, entire to dentate	Lanceolate to lance-oblong, generally entire	Lanceolate to broadly ovate, generally entire
Sepal color	Yellow-green proximally, purple distally	Purple	Light yellow to white	Generally purple
Petal color	Yellow-green proximally, purple distally, especially on veins	Light yellow proximally, light purple distally	Light yellow to white	Purple
Silique shape	Arcuate	Arcuate	Arcuate	Generally straight
Silique dimensions	To 15 cm long, ±2 mm wide	6–14 cm long, 2.5–3.5 mm wide	5–8 cm long, 1.5–2 mm wide	5–8 cm long, 2.5–6 mm wide

high. Basal leaves in rosettes; basal and lowermost cauline leaves petioled, elliptic to suborbicular, obtuse, cuneate at base, blades 1–5.5 cm long, usually dentate with callus-tipped teeth, less commonly entire; cauline leaves to 14 cm long, gradually reduced upward, generally entire or nearly so (the lower occasionally dentate), the lower oblanceolate to broadly strap-shaped, with a winged petiole ± clasping the stem, the middle and upper broadly ovate or broadly oblong to suborbicular, sessile, broadly amplexicaul, the tip often bluntly apiculate with a setose hair. Inflorescence ebracteate, at first dense, becoming lax, simple to rarely branched, 3–7 dm long, pedicels divergent-ascending, thin to stout in fruit, 4–10 mm long. Sepals narrowly oblong, not keeled, 6–8 mm long, lower 2/3 yellow-green, upper 1/3 purple, scarious-margined distally or throughout, with a tuft of simple, stout, broad-based trichomes just below tip. Petals narrowly linear-spatulate with tip ± acuminate, 10–12 mm long, channeled, not or scarcely crisped, claw ± spatulate-oblanceolate, wider than blade, with constriction at junction, blade scarious-margined, bottom 2/3 yellow green and upper 1/3 purplish especially on veins, the upper two petals recurved. Filaments all free, in three pairs of unequal length, the anthers of the longest (adaxial) pair somewhat reduced. Style 1.5–3.5 mm long; stigma ± entire. Siliques ± spreading, weakly to very strongly arcuate, strongly flattened parallel to the replum, ±2 mm wide, up to 15 cm long. Seeds brown, orbicular to ovate or oblong, compressed, narrowly wing-margined, 2–3 mm long; cotyledons accumbent.

Paratypes. USA, California: Butte Co.: ca. 4 km SSW of Big Bar Mtn. on N side of Forest Service Rd. 22N84, T22N R5E SW1/4 of NW1/4 S20, 1006 m, 6 July 1993, B. Castro et. al. 465 (CHSC, UC); 4 km S of Stirling City, 1100 m, 17 September 1983, L. Ahart 4434 (CHSC, MO); north of Cohasset near county line, T24N R2E NE 1/4 S1, 1097 m, 11 June 1981, R. A. Schisling 4085a (CHSC); NW side of canyon of Cedar Ck., 6.6 km E of Lomo along the "Cedar Loop", T25N R3E SE 1/4 S11, 1280 m, 14 June 1988, L. P. Janeway 2791 (CHSC); on Carpenter Ridge, ca. 3.2 km SW of Butte Meadows, T25N R3E NW 1/4 S1, 1340 m, 11 June 1981, R. E. Preston 83 (CHSC); near Humboldt Rd., ca. 5 km SW of Butte Meadows, 1450 m, 16 August 1983, L. Ahart 4283 (CHSC, MO); on side of Old Humboldt Rd., ca. 1.4 km W of Butte Meadows Forestry Station, 1341 m, 6 July 1980, M. S. Taylor 3074 (CHSC); Tehama Co.: on roadbanks along Hwy. 32 ca. 4.8 km E of Soda Springs Rd. and 16 km E of Lomo, 8 September 1967, A. Kruckeberg 6042 (WTU); along CA Hwy. 32, ca. 5.5 air km NNW of Butte Meadows, T27N R3E bdy. NW, NE1/4 of NE1/4 S36, 1189 m, 3 October 1989, R. E. Buck 1414 (UC); Shasta Co.: Tamarack Road near summit, 9 July 1898, M. S. Baker 413 (UC); N side of Bluejay Mtn. along rd. to Hogback Mtn. lookout, T35N R1W SE1/4 of SW1/4 S18, 884 m, 4 October 1989, R. E. Buck 1415 (UC); along dirt rd., W-facing slope just below ridgetop on E side of Stump Ck. cyn, T37N R1W NE1/4 of SE1/4 S11, 716 m, 25 June 1987, R. E. Buck et. al. 711 (UC); upper W-facing slope just below saddle bet. Stump Ck. Butte summit and hill to S, T37N R1W NE1/4 of SE1/4 S3, 1173 m, 24 June 1988, R. E. Buck & R. Palmer 1016 (UC).

DISTRIBUTION AND HABITAT

Streptanthus longisiliqus occurs on the western slope of the extreme northern Sierra Nevada in

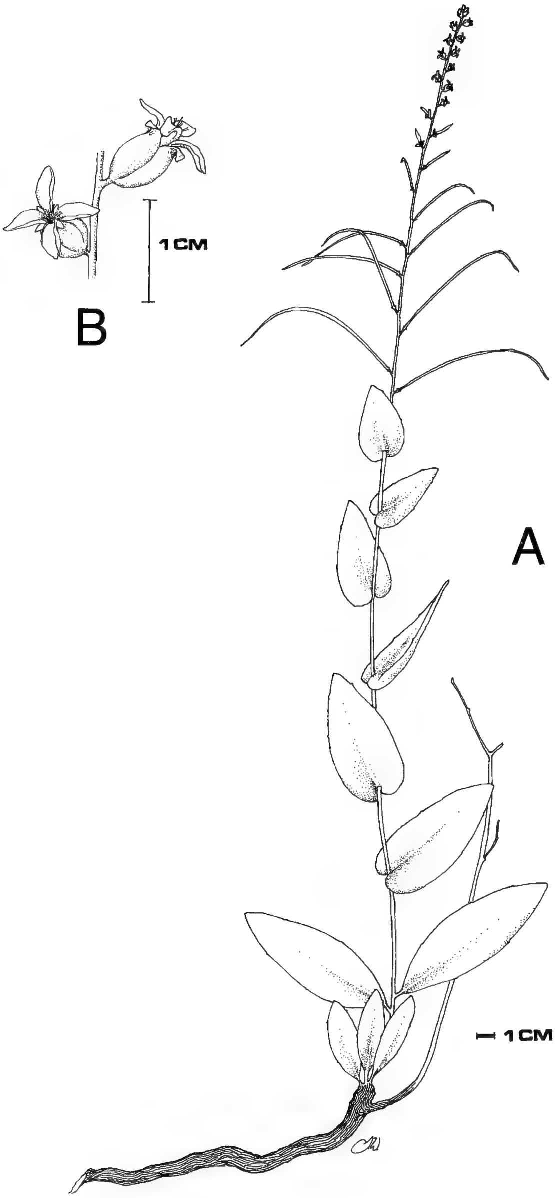

FIG. 1. *Streptanthus longisiliqus*. A) Habit, with flowers and immature fruits; B) Flowers.

eastern Butte and Tehama Cos., California, and in the eastern Klamath Mountains/extreme southern Cascade Range border region to the north in central Shasta Co., California (Fig. 2). It occurs at elevations from 715 to 1500 m. It does not seem to have any substrate preferences, occurring on a variety of igneous, sedimentary, and metamorphic substrates. Within its range, it appears to be relatively uncommon and sporadically distributed, with widely scattered, localized populations seldom containing more than 100 plants, and often with less than 50. The species appears to be absent from most of the apparently suitable habitat within its range.

Streptanthus longisiliqus generally occurs in lower montane coniferous forest, typically dominated by such tree species as *Pinus ponderosa* Douglas ex P. & C. Lawson, *Calocedrus decurrens* (Torr.) Florin, *Pseudotsuga menziesii* (Mirbel) Franco, *Quercus chrysolepis* Liebm., and *Quercus kelloggii* Newberry. At one location on Bluejay Mountain in Shasta Co., the species occurs in an extensive forest overwhelmingly dominated by *Q. kelloggii*. It generally occurs in localized openings within the forest. The species is tolerant of some disturbance and may be favored by it. It often occurs in some numbers on roadcuts, and it is sometimes observed to be relatively abundant on roadcuts and rare but widely scattered in the surrounding undisturbed forest.

Associated shrubs include *Ceanothus integerrimus* Hook. & Arn., *Toxicodendron diversilobum* (Torr. & Gray) Greene, and *Symphoricarpos mollis* Nutt. Associated subshrubs and herbs include *Chamaebatia foliolosa* Benth., *Eriogonum nudum* Dougl. ex Benth., *Osmorhiza chilensis* Hook. & Arn., *Malacothrix floccifera* (DC.) Blake, *Eriophyllum lanatum* (Pursh) Forbes, and *Melica harfordii* Boland.

Taxonomic Relationships

Streptanthus longisiliqus is a member of subgenus *Pleiocardia* (Greene) Jepson, which encompasses mostly biennial to perennial species occurring in the western United States (west of the Rocky Mountains) and adjacent northern Mexico, with stamens free to the base and the anthers of the adaxial stamen pair the same size as those of the other two pairs of stamens or somewhat reduced (>1/2 the length). The more specialized subgenus *Euclisia*, the other subgenus occurring in western North America, consists of mostly annual species with the filaments of the adaxial stamen pair partially to completely connate and the anthers greatly reduced and often sterile (Kruckeberg and Morrison 1983). Within subgenus *Pleiocardia*, Rodman et al. (1981) informally recognized two groups, Cordati and Tortuosi. *Streptanthus longisiliqus* clearly falls within Cordati, characterized by an ebracteate inflorescence, cauline leaves generally strongly reduced upwards (except in *S. barbatus* S. Watson), and sepal tips generally bristly with stout, broad-based trichomes (except in *S. howellii* S. Watson).

Within the informal group Cordati, *S. longisiliqus* appears to be most closely related to *S. campestris* and *S. bernardinus*. These three species are distinguished from other members of the informal group Cordati by their similarity in habit and by their strongly arcuate fruits. Table 1 compares the three species morphologically, and also includes *S. cordatus* var. *cordatus*, since some previous collections of *S. longisiliqus* have been

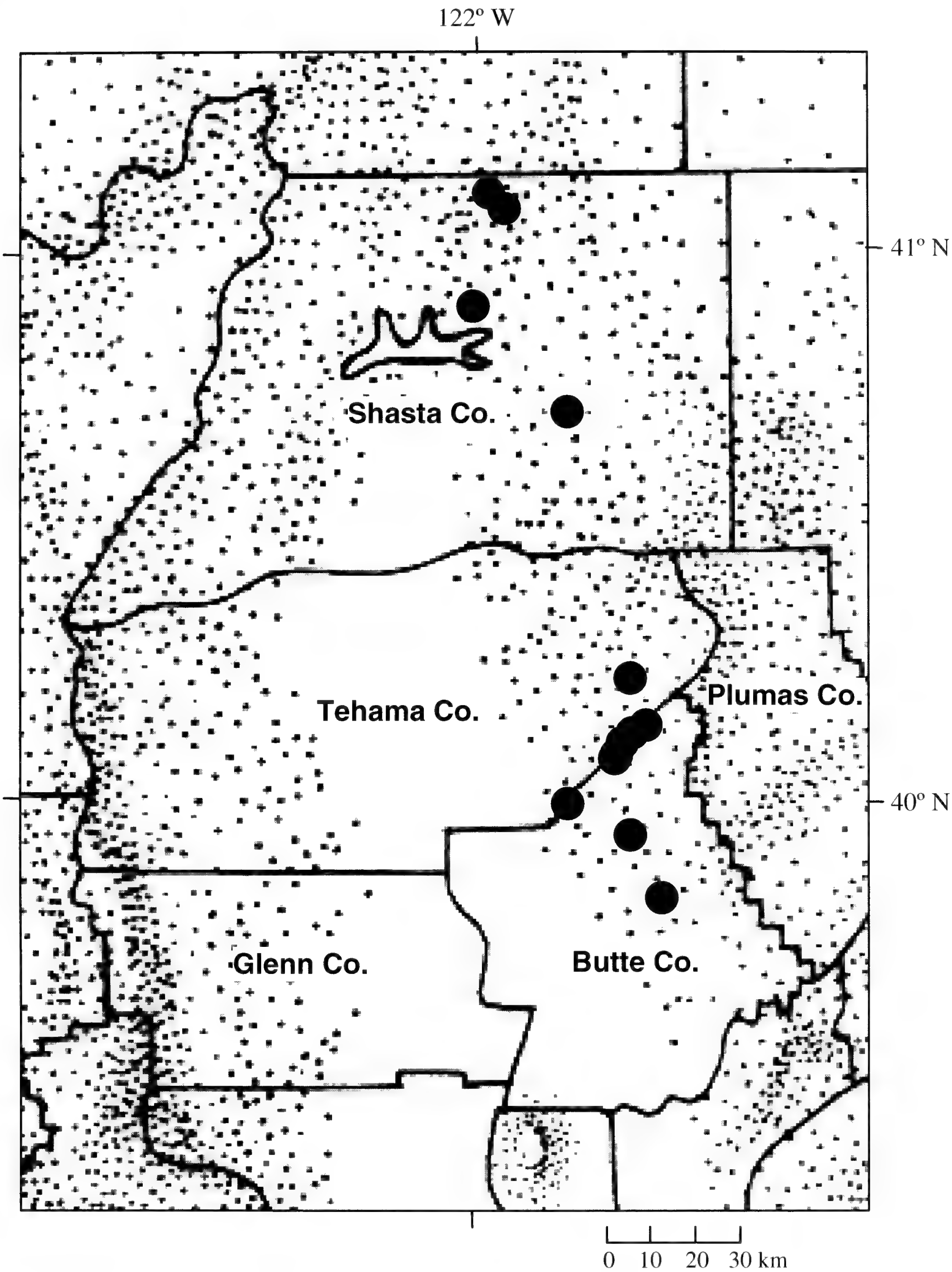

FIG. 2. Distribution of *Streptanthus longisiliqus* in northeastern California.

identified as that taxon. Most other members of Cordati have the fruits straight or only slightly arcuate. *S. barbatus* S. Watson also sometimes has strongly arcuate fruits, but that species is readily distinguished from the former three species by its broadly ovate to orbicular, more or less overlapping cauline leaves that are scarcely reduced upward, as well as by its generally more erect, less branched habit. *Streptanthus longisiliqus*, *S. campestris*, and *S. bernardinus* also occur in similar habitats. The montane coniferous forests in which *S. longisiliqus* occurs are northern analogues of the southern California montane coniferous forests in which the former two species occur and contain many species in common with them.

Streptanthus bernardinus is the most distinctive of the three arcuate-fruited species because of its

yellow sepals and petals and generally smaller stature (stems <7 dm high; *S. campestris* and *S. longisiliqus* to 15 dm). *Streptanthus longisiliqus* closely resembles *S. campestris* in most respects, differing in its ovate to suborbicular, generally entire middle and upper cauline leaves and generally glabrous petioles of the basal and lower cauline leaves. In *S. campestris*, the middle and upper cauline leaves are lanceolate to lance-oblong and entire to dentate, and the petioles (and, often, the leaf margins) of the basal and lower cauline leaves are generally ciliate.

Rarity and Conservation Status

Streptanthus longisiliqus is a species of limited distribution; it occurs in only three counties, and its range extends only approximately 160 km north-south. Within its range, it is uncommon and sporadic in its occurrence. Although some populations are along well-traveled roads, many of the known localities are remote. The species is somewhat tolerant of disturbances, such as grading and excavating, and may even be favored by such disturbances if they are localized. However, logging activities and off-road vehicles constitute potential threats to the species.

Given the distribution of *S. longisiliqus*, the remoteness of many of the known localities, the species' tolerance of disturbance, and the nature and level of potential threats to the species, *S. longisiliqus* should not be considered endangered at present. However, the species is uncommon enough that its status should be monitored. We recommend that *S. longisiliqus* be considered for inclusion on List 4 (Plants of Limited Distribution—A Watch List) of the California Native Plant Society's (CNPS) Inventory of Rare and Endangered Vascular Plants of California (CNPS 2001).

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REVIEW

Plants on Islands: Diversity and Dynamics on a Continental Archipelago. By MARTIN L. CODY. 2006. University of California Press, Berkeley, CA. 315 pp. Hard Cover $49.95. ISBN 978-052024729-1.

Barkley Sound is a large embayment on the west side of Vancouver Island, British Columbia. It contains over 200 islands of various sizes. Based on a field study that extended nearly 25 yr, Martin Cody of UCLA has compiled an enormous data set on diversity and dynamics of some 300 species of plants that inhabit the islands of Barkley Sound. In this book, these data have been exploited in every imaginable way in order to test the concepts and theories of island biogeography. Four appendices at the back of the book include lists of plant species, bird species, and a gazetteer of Islands.

In his introduction, Cody reviews the history of island biogeographic studies beginning with Sir Joseph Hooker's presentation in 1846 to the Linnaean Society on the flora of the Galapagos Islands. Using Hooker's initial contributions to the understanding of islands, Cody lays out the framework for his studies on the plants of the islands in Barkley Sound, pointing out that these are continental islands, not oceanic islands, hence he will say little about endemism, radiations, and relicts. In the introduction, he also states that this book, "…is in no way intended to be a review, or overview, of island biogeography, ecology, or evolution, or of island plant biology." He then lists his "personal favorites" of all the literature he deems relevant to the science of island biology, a list in itself that should be useful to anyone interested in the biogeography of island plants.

Having made that disclaimer in the introduction, Cody then goes on, particularly in Chapter 3, to write an excellent overview of the theory, concepts, and analytical tools of island biogeography, emphasizing chiefly the aspects of colonization and extinction dynamics of continental islands. He pays tribute to the work of R. H. MacArthur and E. O. Wilson, who in the 1960s laid out the principles of the "equilibrium theory of island biogeography." This well know theory, referred to by Cody as the "M/W model," balances immigration and extinctions rates as a function of number of species. With a series of graphs, Cody clearly describes how the M/W model applies to islands of various sizes and distances from the mainland. This chapter, by itself, is a valuable contribution to the literature about island plants. It is illustrated with graphs and data, all of which are eloquently explained, and his use of statistics will not overwhelm the reader.

The rest of the book is specifically about the islands of Barkley Sound. Chapter 2 is an excellent introduction to the geography, geology, history, climate, and general ecology of the region. Of particular interest is his discussion of the flora and vegetation of the "Coastal Coniferous Forest." This community, distributed from southeastern Alaska to northern California, is also referred to by many authors as the "Temperate Rainforest," Many people think if these forests, which include the largest terrestrial organisms on earth, as one of North America's treasures. Readers who may not be familiar with wet coastal forests, will gain an appreciation for the diversity and significance of this community to the biota of the world.

Chapters 4 through 8 deal specifically with the islands of Barkley Sound. Each chapter analyzes the plants on these islands from a perspective of the M/W model of MacArthur and Wilson. Chapter 4 is about species numbers, island size, and isolation. Chapter 5 on "nestedness and assembly rules" analyzes the distribution of species within different habitats. Chapter 6 deals specifically with "turnover rates," in which the balance between colonization and extinction on these islands is described. Chapter 7 is about the various mechanisms and dynamics of dispersal responsible for the species on these islands. It is particularly interesting in its documentation that, over time, dispersal capacity on the islands becomes reduced in wind-dispersed members of the Asteraceae. Chapter 8 is about the impact and evolution of non-native species. He points out that "weedy aliens" colonize primarily edge habitats or disturbance sites, and they evolve rapidly, typically losing significant dispersal capacity over a period of decades. Here, Cody is able to generalize about the influence of non-native colonizations on depauperate island floras. Also in Chapter 8 he analyzes data that show evolutionary shifts in two species of animals, deer mice and banana slugs. Deer mice on Willis Island were almost 20% heavier than those on the mainland, an example of gigantism that often is demonstrated by rodents on islands in other parts of the world. The extensive discussion of evolution in spotting patterns of banana slugs is particularly interesting. Banana slugs, relict species which are virtually unable to cross seawater barriers, have evolved on these islands for about 10,000 yr. During that time, it appears that the unspotted morphs evolved in association with open habitats where they tend to be more suitably adapted to warm, dry conditions. In these five chapters, loaded with graphs and statistics, Martin Cody illustrates how a scientist can exploit his data. He does it wonderfully, never failing to explain how the data fit the concepts he is analyzing.

Chapter 9, the final chapter, is a synopsis subtitled "Lessons from a Continental Archipelago." In this chapter, Cody summarizes what he learned about the evolutionary and biogeographic picture of the islands in Barkley Sound. Once again, he generalizes about the relevance to biogeographic theories, particularly with respect to the M/W model. He talks about phenomena that fit his expectations and those that didn't. He finishes up by emphasizing what seemed most important to biogeographic theory of islands.

This book is an invaluable addition to biological literature. Based on nearly a quarter-century of research, it clearly depicts the flora of the islands in Barkley Sound and applies the data to processes of evolution and biogeography as they apply to continental islands in general. Furthermore, it is an important resource that characterizes one of North America's significant plant communities, the moist coastal coniferous forest of the Pacific Northwest. Every biologist with an interest in islands or the spectacular forests of the Pacific Northwest should own this book.

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MADROÑO, Vol. 54, No. 1, p. 101, 2007

NOTEWORTHY COLLECTION

OREGON

HAINARDIA CYLINDRICA (WILLD.) GREUTER (POACEAE).—Curry Co., along U.S. Hwy. 101 by its junction with Pistol River Loop Road ca. 17.6 km south of Gold Beach, in sandy soil with *Lotus*, *Juncus*, *Plantago*, *Briza*, *Melilotus*, *Parentucellia*, *Festuca*, 20 m, 42°16′7.2″N, 124°24′4.1″W, 15 June 2005, *R.R. Halse 6773* (OSC, UTC, duplicates to be distributed).

Previous knowledge. This European native is known from California and Baja California, Mexico (J.C. Hickman, ed., 1993, The Jepson Manual: Higher Plants of California).

Significance. First report from Oregon.

PSEUDOGNAPHALIUM LUTEOALBUM (L.) HILLIARD & BURTT (=*GNAPHALIUM LUTEOALBUM* L.) (ASTERACEAE).—Coos Co., along State Hwy. 42 ca. 16.8 km east of Bridge, weedy roadside with *Cynosurus*, *Rubus*, *Daucus*, *Cytisus*, *Avena*, *Mentha*, 139 m, 42°57′48.5″N, 123°50′53.2″W, 13 June 2005, *R.R. Halse 6753* (OSC); Curry Co., along U.S. Hwy. 101 at its junction with Meyers Creek Road ca. 10.5 km south of Gold Beach, weedy roadside with *Holcus*, *Briza*, *Lotus*, *Brassica*, *Linum*, *Rubus*, 34 m, 42°18′24.3″N, 124°24′34.3″W, 14 June 2005, *R.R. Halse 6772* (OSC, duplicates to be distributed); Lane Co., along State Hwy. 126 ca. 5.6 km east of Florence, weedy roadside with *Rubus*, *Hypochaeris*, *Phalaris*, *Carex*, *Juncus*, *Spiraea*, 22 m, 43.99682°N, 124.02306°W, 16 November 2005, *R.R. Halse 6899* (OSC, duplicates to be distributed).

Previous knowledge. This European species is widely distributed in California (J.C. Hickman, ed., 1993, The Jepson Manual: Higher Plants of California). In Oregon it has been collected on ballast in Multnomah Co., Portland, in 1902, *E.P. Sheldon S9905, S10918* (ORE).

Significance. First collections of this taxon in Oregon in over 100 yr and a southwestern range extension of ca. 200–365 km.

—RICHARD R. HALSE, Dept. of Botany & Plant Pathology, 2082 Cordley Hall, Oregon State University, Corvallis, OR 97331.

MADROÑO, Vol. 54, No. 1, pp. 102–104, 2007

NOTEWORTHY COLLECTIONS

SONORA

HERNIARIA HIRSUTA L. subsp. *CINEREA* (DC.) Cout. (CARYOPHYLLACEAE).—Annual on sandy gravel substrate on bank of active channel, Río Sonora at Rancho El Tépari (KM 84 de la Carretera 86), Municipio de Arizpe, 30°12′35″N, 110°14′07″W, 755 m, *J. J. Sánchez E. NF-232*, *L. Moreno M.*, *E. Gómez L.* (14 Mar 2002, USON), det. T. R. Van Devender; locally common annual in sycamore-willow riparian forest in rocky stream canyon, Cañón Planchas de Plata, upstream from Rancho Esmeralda (=Rancho Las Borregas), southeast end of Sierra La Esmeralda, Municipio de Nogales, 31°12′51″N 111°07′21″W, 1090 m, *Van Devender 2005-111*, *P. Merlin*, *K. Krebbs*, *S. Norman* (6 Mar 2005, ARIZ, MEXU); locally common annual in disturbed soil in rocky, grazed area on oak woodland/desert grassland mosaic, Arroyo El Oso, west slope of Sierra de La Madera, 15.7 km (by road) southeast of MEX 15 (in Imuris), Municipio de Magdalena de Kino, 30°41′36″N 110°47′01″W, 1167 m, *Van Devender 2005-786*, *Reina G.* (29 Apr 2005, ARIZ, ASU, CAS, HCIB, MEXU, NMC, SD, USON)

Previous knowledge. Native to Eurasia. Reported from California, Maryland, Massachusetts, New York, Oregon, Pennsylvania, and Wyoming. Common in the Tucson and Phoenix areas in south-central Arizona. *R. S. Felger 03-246* (ARIZ) from Organ Pipe Cactus National Monument in Arizona is close to the Sonoran border. In México occurs in Baja California.

Significance. First report as a weed in disturbed areas for Sonora.

KOCHIA SCOPARIA (L.) Schrad. (CHENOPODIACEAE).—Uncommon annual on roadside, western edge of Agua Prieta on MEX 2, Municipio de Agua Prieta, ca. 31°18′49″N, 109°33′40″W, 1215 m, *Van Devender 2002-614*, *Reina G.*, *S. C. Doan*, *D. Z. Damrel*, *Z. Liu*, *W. A. Marussich* (10 Sep 2002, ARIZ, ASU, HCIB, MEXU, NMC, TEX, USON)

Previous knowledge. Native to Eurasia. Occurs in most of the continental USA and listed as a Noxious Weed in Colorado and Washington, potentially invasive in Connecticut, and a quarantine weed in Oregon. Widespread in the higher elevations of northern and southeastern Arizona, especially in the San Pedro River Valley. In México occurs in Baja California, Chihuahua, Coahuila, Distrito Federal, Estado de México, and Jalisco.

Significance. First report as an agricultural weed in Sonora.

CHORISPORA TENELLA (Pall.) DC. (CRUCIFERAE).—Uncommon annual in sand in wash, flowers purple, 6.3 km S of Fronteras on MEX 17, Municipio de Fronteras, 30°50′45″N, 109°34′23″W, 1166 m, *Reina G. 2003-409*, *Van Devender*, *G. Anderson* (10 Apr 2003, ASU, USON), det. A. Salywon.

Previous knowledge. Native to southern Asia. Occurs in most of the continental USA, listed as a noxious weed in California and Colorado, and an invasive plant in the USA and Canada. Common in fields at higher elevations in Arizona, including some areas in Pima and Cochise Counties close to the Sonoran border.

Significance. First report as an agricultural weed in Sonora and México.

SINAPIS ARVENSIS L. (CRUCIFERAE).—Solitary 1.0 m tall herb in moist soil in canal bottom, flowers bright yellow, Hermosillo, Municipio de Hermosillo, 29°04′54″N, 110°55′24″W, 213 m, *Reina G. 2003-302*, *Van Devender* (14 Mar 2003, ARIZ, ASU, CAS, HCIB, MEXU, SD, TEX, USON); solitary herbaceous perennial in disturbed soil near house, flowers yellow, Nacozari de García, Municipio de Nacozari de García, 30°22′10″N, 109°40′58″W, 1134 m, *Van Devender 2003-537*, *Reina G.* (13 Apr 2003, ARIZ, ASU, USON) det. A. Salywon; locally common annual in disturbed soil, flowers bright yellow, 1.3 km east of Rancho Viejo, Municipio de Ures, 29°07′46″N 110°18′08″W, 462 m, *Reina G. 2005-168*, *Van Devender* (12 Mar 2005, ASU, NMC, USON), det. A. Salywon.

Previous knowledge. Native to Europe. Occurs all over continental and insular USA. Listed as a Noxious Weed in Colorado, Michigan, and Ohio, a secondary noxious weed in Iowa, and an invasive plant in the USA and Canada. Widespread in southwestern Arizona. *V. Roth s.n.* (ARIZ) from near Yuma is close to the Sonoran border.

Significance. First report as an agricultural weed in Sonora and México.

CUCUMIS DIPSACEUS Ehrenb. ex Spach. (CUCURBITACEAE).—Locally common prostrate annual vine on disturbed roadside, Sonoran desertscrub, flowers yellow; fruit green turning yellow, toll station on MEX 15 near Pemex El Valiente, Municipio de Guaymas, 28°02′10″N 110°55′22″W, 41 m elevation, "huevos de gato" fide Mario Lizarraga of Empalme, *Reina* G. 2006-240, T.R. *Van Devender* (3 Mar 2006, ARIZ, ASU, HCIB, MEXU, NMC, USON)

Previous knowledge. Native to Africa. Occurs in Hawaii and Texas in the USA. In México it is reported from Baja California Sur, Jalisco, Nayarit, San Luis Potosí, Sinaloa, Tamaulipas, and Veracruz.

Significance. First report as a weed in disturbed areas for Sonora.

FUMARIA OFFICINALIS L. (FUMARIACEAE).—Locally common annual on disturbed bank, flowers light purple, along the banks of the Río Magdalena, Magdalena, cottonwood willow gallery forest, "huele de noche" (smells at night), Municipio de Magdalena de Kino, 30°37′52″N, 110°58′20″W, ca. 750 m, *Reina G. 98-169*, *Van Devender* (8 Mar 1998, ARIZ, CAS, MEXU, TEX, USON); solitary herb in disturbed soil, flowers light purple, Arroyo Sásabe in Magdalena, Municipio de Magdalena de Kino, 30°37′20″N, 110°58′35″W, 762 m, *Reina G. 2003-181*, *Van Devender* (9 Mar 2003, ASU, HCIB), det. P. D. Jenkins.

Previous knowledge. Native to Europe. Occurs in most of continental USA. Rare in Pima and Santa Cruz Counties in southern Arizona.

Significance. First report as an escape from cultivation in Sonora and México.

FUMARIA PARVIFLORA Lam. (FUMARIACEAE).—Locally uncommon annual, flowers white, Arroyo Sásabe in Magdalena, Municipio de Magdalena de Kino, 30°37′20″N 110°58′35″W, 762 m, *Reina G. 2003-188, Van Devender* (9 Mar 2003, ARIZ, ASU, MEXU, TEX, USON); locally common annual in disturbed area below houses, flowers white, Nacozari de García, Municipio de Nacozari de García, 30°22′10″N, 109°40′58″W, 1134 m, *Van Devender* 2003- 538, *Reina G.* (13 Apr 2003, ARIZ, CAS, HCIB, NMC, USON); locally common annual on roadside, flowers white, western edge of Agua Prieta on MEX 2, Municipio de Agua Prieta, ca. 31°18′49″N 109°33′40″W, 1215 m, *Van Devender 2004-360, Reina G., S. C. Doan, G. M. Ferguson, Z. Liu, J. Anderson, R. Johnson* (24 Apr 2004, ARIZ, USON).

Previous knowledge. Native to Europe. Occurs in Arizona, California, Florida, Oregon, Pennsylvania, and Texas. Uncommon in southern Arizona. *Donndelinger s.n.* (ARIZ) from Yuma is close to the Sonoran border. In México occurs in Coahuila, Distrito Federal, Durango, Estado de México, and Hidalgo.

Significance. First report as an escape from cultivation in Sonora.

ERAGROSTIS ECHINOCHLOIDEA Stapf (GRAMINEAE).—Uncommon perennial under *Schinus terebinthifolia* tree, toll station on MEX 15 bypass at Magdalena, Municipio de Magdalena de Kino, ca. 30°37′N, 110°58′30″W, 800 m, *Van Devender 2001-626, Reina G.* (12 Aug 2001, ARIZ, CAS, HCIB, MEXU, USON), ver. J. R. Reeder.

Previous knowledge. Native to Africa. Introduced in Arizona by the Soil Conservation Service by the early 1940s and common in the Tucson area. *Reeder 7866* (ARIZ) from Bisbee in 1986 is close to the Sonoran border.

Significance. First report as an escaped forage grass in Sonora and México.

ERAGROSTIS SUPERBA Peyr. (GRAMINEAE).—Perennial along dirt road, grassland, Rancho Los Fresnos, 80 m south of Arizona border, south-southwest of the Huachuca Mountains, Municipio de Santa Cruz, ca. 31°19′53″N 110°23′30″W, 1577 m, *G. Valencia O. [Reina G. 2005-1663]* (22 Jun 2005, ARIZ), det. T. R. Van Devender.

Previous knowledge. Native to Africa, Australia, India, and South America. Occurs in Arizona, California, Hawaii, New Mexico, and Texas. Cultivated and seeded in southern Arizona in the 1940s and common today in south-central Arizona, especially along the border in Santa Cruz and Cochise Counties. *Van Devender* 95-501 (ARIZ, USON) from Nogales near border crossing and *Reina G.* 2005-1656 (ARIZ) from Naco are close to the Sonoran border. Established in an agriculture station in central Chihuahua (Toutcha Lebgue, pers. comm., 2005).

Significance. Although Beetle and Johnson (1991. Gramineas de Sonora, Secretaría de Agricultura y Recursos Hidraulicos, Hermosillo) reported this distinctive grass from agricultural settings in four Municipios in northern Sonora, we have collected extensively in these areas and have not observed the species, and there are no specimens at ARIZ, MEXU (Leticia Torres-Colín, pers. comm., 2007), or USON (Jesús Sánchez-Escalante, pers. comm., 2007) herbaria. Specimens may be in COCA in Hermosillo, but this collection is closed. This report documents this escaped forage grass in Sonora.

PENNISETUM SETACEUM (Forssk.) Chiov. (GRAMINEAE).—Locally common ornamental clump grass in garden, spreading rapidly, Hotel la Posada, Alamos, Municipio de Alamos, 27°01′N 108°50′W, 360 m, *Van Devender 2005-8, M. A. Dimmitt, G. Montgomery* (21 Jan 2005, ARIZ); solitary large clump on edge of sidewalk, others planted in yards and PEMEX station garden, said to have recently been brought from Tucson, AZ; Madgalena, Municipio de Magdalena de Kino, 30°37′34″N 110°57′58″W, 773 m, *Reina G. 2004-976, Van Devender, M. A. Dimmitt, C. Barclay, T. Bean* (24 Aug 2004, ARIZ, MEXU, USON) ver. J. R. Reeder.

Previous knowledge. Native to Ethiopia. Occurs in Arizona, California, Colorado, Florida, Hawaii, Louisiana, Nevada, New Mexico, and Tennessee. Listed as a Noxious Weed in Hawaii and Nevada, and an invasive plant by the California Exotic Pest Plant Council. Cultivated in Tucson, Arizona, since the late 1940s, and now common in the Tucson and Phoenix areas. *Van Devender* 2004-1044 (ARIZ, ASU) from Santa Cruz County is close to the border. In México occurs in Baja California.

Significance. First report as an escape from cultivation in Sonora.

ASPHODELUS FISTULOSUS L. (LILIACEAE).—Cultivated herbaceous perennial brought from nearby water tank, escaping around house, flowers white, Rancho Cerro Prieto, Cerro Prieto, ca. 10 km (by air) NE of Cucurpe, Sonoran desertscrub on rocky slope, Municipio de Cucurpe, 30°25′20″N, 110°39′31″W, 1150 m, *Reina G. 2002-325, Van Devender, K. Krebbs, G. Anderson* (16 May 2002, ARIZ, USON)

Previous knowledge. Native to Eurasia. Occurs in Alabama, California, Florida, Massachusetts, Minnesota, New Mexico, North Carolina, Oregon, South Carolina, Texas, and Vermont. A Federal Noxious weed. It is rare in south-central Arizona. In México occurs in Coahuila, Durango, Estado de México, Guanajuato, Hidalgo, Nuevo León, Querétaro, San Luis Potosí, Tamaulipas, Tlaxcala, and Veracruz.

Significance. First report as an escape from cultivation in Sonora.

GLAUCIUM CORNICULATUM (L.) Rudolph (PAPAVERACEAE).—Ca. 10 annuals on disturbed roadside, petals rose-red at base grading to burnt-orange on tips, oblong purple spot at base of petal visible inside and out, 4.7 km NE of Santa Ana on MEX 15, Municipio de Santa Ana, 30°34′34″N, 111°04′50″W, 650 m, [seen in two other localities between Santa Ana and Magdalena] *Reina G. 98-417, Van Devender* (10 Apr 1998, ARIZ, CAS, MEXU, NY), ver. T. F. Daniel; locally common annual, flowers dark orange-red with dark spots inside, some flowers with more yellow, western edge of Agua Prieta on MEX 2, Municipio de Agua Prieta, ca. 31°18′49″N 109°33′40″W, 1215 m, *Van Devender 2004-334, Reina G., S.C. Doan, G.M. Ferguson, Z. Liu, J. Anderson, R. Johnson* (24 Apr 2004, ASDM, ASU - Doan collection, USON)

Previous knowledge. Native to Eurasia. Occurs in Kansas, Montana, Nevada, New York Oregon, Pennsylvania, and Texas. The only Arizona collection from Hwy 80 in Cochise County (2001, *S. Rhodes 181*, ASC)

is close to the border just north of the Agua Prieta population.

Significance. First report as roadside weed in Sonora and México.

VERBASCUM VIRGATUM Stokes (SCROPHULARIACEAE).—Uncommon perennial herb on disturbed roadside near houses, flowers yellow, Agua Prieta, Municipio de Agua Prieta, 31°18′49″N, 109°33′24″W, 1214 m, *Reina G. 2002-300*, *Van Devender*, *K. Krebbs*, *G. Anderson* (14 May 2002, ARIZ, USON)

Previous knowledge. Native to Europe. Occurs in Arizona, California, Florida, Hawaii, Idaho, Illinois, Indiana, Louisiana, Nevada, New Mexico, New York, North Carolina, Ohio, Pennsylvania, South Carolina, Texas, and Utah. Common in the highlands of north-central and southeastern Arizona. *McLaughlin 8306* (ARIZ) from the San Rafael Valley, Santa Cruz County is very close to the Sonoran border. In México occurs in Baja California Sur, Distrito Federal, Estado de México, Hidalgo, Querétaro, and Tlaxcala.

Significance. First report as roadside weed in Sonora.

—THOMAS R. VAN DEVENDER AND ANA L. REINA G, Arizona-Sonora Desert Museum, 2021 N. Kinney Road, Tucson, AZ 85743.

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ERRATA

The illustration of *Calamagrostis tacomensis* on Madroño 53:293 was prepared by Cindy Roché and Hanna Pazdîrková. The copyright is held by Utah State University. This information was inadvertently omitted from the article (Marr and Hebda 2006).

Also, in the description of *Calamagrostis tacomensis*, on page 293, "Haplotype" should be "Holotype."

MARR, K. L. AND R. J. HEBDA. 2006. *Calamagrostis tacomensis* (Poaceae): a new species from Washington and Oregon. Madroño 53:288–298.

Volume 54, Number 1, pages 1–104, published 3 July 2007

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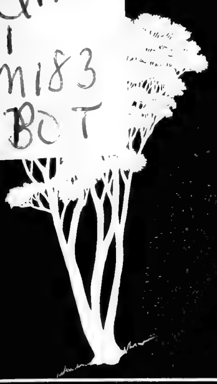

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MADROÑO

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CONTENTS

NOTES

NEW SPECIES

PUBLISHED QUARTERLY BY THE CALIFORNIA BOTANICAL SOCIETY

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SPATIOTEMPORAL PATTERNS IN THE NON-NATIVE FLORA OF CALIFORNIA, USA[1]

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ABSTRACT

Economic and ecological problems brought by the invasion of non-native species can be prevented in part by identifying patterns in the invasion process. We tested hypotheses that address variation in the spatial, taxonomic, and temporal distributions of non-native floras in the large and diverse geographic area defined as California. Analyses reveal that in time, 79% of all non-native species will occur in disturbed habitat; polyploidy is not correlated with geographic spread; the Poaceae and Brassicaceae are the most broadly represented families across elevations; introductions increase from all geographic regions from 1925 to 1969, but more recently from Asia, Australia, Africa, South Africa, and South America; and more than 50% of all alien taxa recorded prior to 1925 have become widespread. Some taxa without native representatives contain some of the worst invaders in the flora, thus we suggest that control efforts should be directed to recent arrivals without native representation. Our conclusions support the need to control the spread of non-natives early in the invasion process but also emphasize the need to control invasions from a floristic perspective, both locally and regionally.

Key Words: Biological invasions, California, distribution, disturbance, historical, non-native flora, polyploidy, taxonomy.

Biotic invasions are an increasing economic problem, costing billions of dollars in damage and control. Likewise, they are an increasing conservation problem, altering ecosystems, and endangering other species. But, generally, for any given location, only a fraction of species that are introduced become naturalized, and only a fraction of those that become naturalized become invasive (Williamson 1993). The term "invasive species" as used here is consistent with the Clinton administration criteria (Executive Order 13112, 1999) that include "an alien species whose introduction is *likely* to cause...harm..." (emphasis added). "Harm" however, is a subjective term and whether alien species are legally defined as invasive or less intrusively, simply widespread, there is a need for the identification of those species that readily spread outside their home range (Ewel et al. 1999; Williamson 1999; Mack 2003). All invasive species move through the sequence of introduction, casual reproduction, naturalization, and, ultimately, invasion (Richardson et al. 2000).

A number of methods have been used to identify potentially invasive taxa and habitats that may be vulnerable to invasion. These approaches include the correlation of organismal characteristics (Baker 1962; Bazzaz 1979), habitat characteristics (Crawley 1987), or both (summarized in Levine et al. 2003) to successful invasives. Some success has been made in the detection of the underlying causes of plant invasions (Mack 2000). For example, successful predictions for which *Pinus* species become invasive can be made from traits such as maximum height, longevity, seed mass, percent germination, interval between seed crops, degree of serotiny, and fire tolerance (Rejmánek and Richardson1996; Richardson and Rejmánek 2004).

Habitat characteristics, ecosystem processes, and ecological interactions increasingly are being considered in a variety of invasion scenarios. Shea and Chesson (2002) emphasize that more advanced stages of community succession and higher levels of species diversity are important ecological factors that can provide some resistance to biological invasions. Pyšek et al. (1995) emphasized that traits that favor invasion success will be different in different habitats.

An analysis of all documented immigrant species over time in a well-studied region allows the identification of non-native species that became invasive to be distinguished from those that are present but did not become either widespread or invasive. Analyses that include both historical and current distribution data for non-native species (Kowarik 1995; Reichard and Hamilton 1997; Pyšek 2001; Duncan and Wil-

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liams 2002; Pyšek et al. 2002, 2003) have been valuable in the identification of potentially problematic taxa and vulnerable habitats. Although likelihood of spread is a function of many variables, without historical analysis, it is impossible to know from a single snapshot in time whether non-invasive species at the moment simply have not had the time or ecological circumstances to spread. The relatively thorough historical documentation of the native and non-native flora of California offers a special opportunity to analyze a large and diverse natural area and explore the fate of the non-native flora through time and space.

California's combination of historical human activity with its topographic, climatic, and native edaphic diversity have made it particularly vulnerable to the spread of non-native taxa (Rejmánek and Randall 1994, 2004). The known current distribution of non-native species and the approximate known time of their introduction make California ideal for understanding the factors that lead to eventual widespread abundance of a non-native species (Hobbs and Humphries 1995; Kowarik 1995). Unfortunately, comparative data for the native flora of California are not similarly databased, so we cannot provide extensive parallel analyses of the non-native flora. This latter comparison remains essential in determining how aspects of the non-native flora of California may differ from the native flora. Kolar and Lodge (2001) suggest comprehensive studies of regional floras will allow for the detection of those traits that may be useful in the prediction of those species that may become widespread or invasive. Nonetheless, much can be made of the data that are available.

Our purpose is to identify spatial, ecological, or taxonomic patterns in plant invasions by providing a historical perspective of non-native species characteristics and their distribution. We compare the presence of the 1338 non-native species, subspecies, and varieties, in the recent California flora of Hickman (1993) supplemented by the list of non-natives of Hrusa et al. (2002) with the presence of the same species in Jepson's 1925 floristic manual for California and Munz and Keck's 1959 California flora and supplement (Munz 1968). We address correlates of invasiveness for California's contemporary 1338 non-native taxa with a refined list of taxa, some of which had less than a decade to establish and others that have been present since at least 1925. The number of non-native taxa in each of the six floras is summarized in Table 1. Within the context of approximate time since introduction, generalized habitat characteristics, and historical and current distribution patterns, we test hypotheses that address the following: whether some taxa are more likely to invade than others;

TABLE 1. NUMBER OF NON-NATIVE SPECIES PRESENT IN THE CALIFORNIA FLORA (HOLLAND AND KEIL 1995).

Year	Number of non-native species	Reference
1925	292	Jepson 1925
1959	725	Munz 1959
1968	874	Munz and Keck 1968
1993	1023	Hickman 1993
2002	1338	Hrusa et al. 2002

whether the non-native flora of California disproportionately originated from certain geographic regions; which habitats have the largest representations of alien taxa; whether polyploidy is an important factor in the success of alien taxa; and finally, whether there is a predictable time between introduction and spread for non-native taxa. The necessary elucidation of predictive hypotheses regarding invasive species is illustrated by observations such as those that indicate high elevation habitats are more vulnerable to invasion from alien species than low elevation habitats (Stohlgren et al. 2002). However, Keeley et al. (2003) found that although the number of alien species declines with increasing elevations, the number of native species also declines. Kowarik (1995) established that the time from introduction of a non-native taxon to invasion can vary widely yet it is not clear whether broad generalizations can be made about the time to invasiveness in California. Additionally, despite the acknowledgement that most angiosperms are polyploid (Grant 1981; Soltis and Soltis 2000), we do not know if polyploid taxa are more likely to colonize new habitats relative to non-polyploids. Stebbins (1971) hypothesized that partial or complete genome duplications within taxa may provide the bases for rapid adaptive response and thus the potential for broader ecological amplitude, but this has not been broadly supported via floristic surveys.

Our Study System

California's topography ranges from 85 m below to 4420 m above sea level, has 1600 km of coastline, a land area of 411,000 km^2, and latitudes from 33°–42° North. Recognizing the pre-Columbian flora of California "recently" evolved with post-Pleistocene climatic change and human disturbance for thousands of years, we define "native" plant species as taxa present prior to European settlement in the 18th century. The earliest extant plant collections of California were made by Brewer and Bolander shortly following statehood in 1849, but are late relative to the European settlement history of the geographic area (Ertter et al. 1995). Descriptions of California's flora were made after expansion into western North America began in earnest, but

these broad floras include much of western North America (e.g., Pursh 1814; Nuttall 1818; Torrey and Gray 1843; Parry 1859). One of the first floras to focus primarily on California was published by Rattan in 1879, containing 600 species. The first comprehensive flora was Jepson's (1925) *Manual of the Flowering Plants of California*, the primary reference for over thirty years, followed by *A California Flora* (Munz and Keck 1959) and supplement (Munz 1968). Most recently, a consortium of authors published *The Jepson Manual of Higher Plants in California* (hereafter "Jepson Manual") (Hickman 1993), with 4839 native and 1023 non-native taxa at the species level or below (784 dicots, 235 monocots, 4 ferns). Hrusa et al. (2002) published a supplement to the Jepson Manual of an additional 315 non-native species, subspecies and varieties.

Materials and Methods

All species indicated as non-native in the Jepson Manual (Hickman 1993) and Hrusa et al. (2002) were entered into a database with the following fields: name, geographic origin, habitat, elevational range, chromosome number, and number of counties occupied. (Some other types of organismal information were not available frequently enough to provide a meaningful analysis, such as seed size, fruit size, mode of dispersal, and pollination mechanism.) The total number of taxa varied in the analyses because among floras we did not differentiate those taxa that had been variously combined within or split from a species. All taxa (and their synonymous names) were then checked for presence in Jepson (1925); Munz and Keck (1959), and its supplement (Munz 1968). The default taxonomic classification used for each taxon was from the Jepson Manual (Hickman 1993), as updated by Hrusa et al. (2002).

Rejmánek et al. (2005) found evidence that taxa without native representation are more likely to become invasive than those with native genera or families (see also Darwin 1859), thus we asked whether that trend holds true for California. We used Z-tests to test the hypotheses that families with no native taxa, and those with the largest representation in the non-native flora, are disproportionately represented.

DiCastri (1989) suggested that the Mediterranean region has provided more invasive taxa to western North America than other geographic regions. Similarly, Pauchard et al. (2004) suggest that floristic comparisons between climatically similar regions will provide a useful basis for monitoring immigrant plant taxa. In addition to Hickman (1993), we used a number of references (USDA 1971; Oswald 1994; Still 1994; Armitage 1997; Bailey 1997; Dirr 1998; Brenzel 2001) to determine the geographic origin of each non-native taxon and assess which geographic regions of the world have contributed the greatest number of alien species to California.

Human-altered habitats are vulnerable to colonization by non-native taxa (Vitousek et al. 1997), thus we examined whether there is a relationship between geographic spread and whether a taxon's habitat is considered disturbed. Although more detailed habitat information beyond that provided by Hickman (1993) and Hrusa et al. (2002) was available for many of the taxa we examined, we found it was not possible to obtain detailed habitat information for most taxa.

Habitat designations provided by floras are limited and have not been subjected to any objective criteria as recommended by Pyšek et al. (2004a, b), but they also provide the greatest consistency of terminology across the largest number of taxa. Terms to describe habitat occurrence within Hickman (1993) can be ambiguous, sometimes indicating distribution and other times, habitat conditions. For example, "disturbed", "invasive", "common", and "abundant weed" are often used synonymously and here are included in the "disturbed" category. Therefore, for the purpose of statistical analyses, we standardized the habitat information provided by Hickman (1993) and Hrusa et al. (2002) and divided habitat codes into four general categories.

Disturbed

Includes, but not limited to: Disturbed areas; open, disturbed sites; disturbed places; disturbed agricultural areas; abundant weed; fields; open ground; widespread; waste places; common; weedy; roadsides; ditch margins; noxious weed; and invasive.

Disturbed, Uncommon

Includes, but not limited to: Uncommon, disturbed areas (or sites or soils); uncommon, waste places; disturbed ground, waif (occasional); uncommon, noxious weed.

Habitat Specific

Includes, but not limited to: beach dunes; sandy soils; wet areas; common weed in moist places; uncommon (low local frequency, but widespread) in wet places; vernal pools; marshes; pond margins; wetlands; woods near coast; coastal scrub; streams and riparian woodlands; meadows; alkaline or saline soils, creekbeds, invasive in shady places; redwood forest.

Habitat Specific, Uncommon

Uncommon, waste places near coast; uncommon (low local frequency, not widespread) in

moist places; waif in meadows; uncommon, wetlands; uncommon, brackish mud flats; uncommon, adobe soils; uncommon, coastal; uncommon wet places.

We tallied the number of non-native taxa present in elevational ranges of $\leq$100 m, $\leq$500 m, $\leq$1000 m, $\leq$2000 m, and $\leq$3000 m to test the hypothesis that higher elevation habitats are being colonized by alien species as often as lower elevation habitats.

We conducted a linear regression analysis to test the hypothesis that there is a relationship between geographic spread and polyploidy, using chromosome number as the dependent variable and number of counties as the independent variable. Stebbins (1971) discerned that polyploidy in plants is based on a base chromosome number greater or equal to x = 6, 7, or 8 and later authors have concurred (Grant 1981; Soltis and Soltis 2000). Grant (1981) used x = 7 to estimate the frequency of polyploidy in the traditionally classified dicots as 48%, monocots 60%, and for all angiosperms 52%. However, because there is some ambiguity in the use of $2n$ = 14 as the "magic" polyploid number, we assigned the taxa in this study to three categories, $2n \leq 12$, $2n$ = 14–18, and $2n \geq 20$. Chromosome numbers not found in Hickman (1993) were supplemented by Radford *et al.* (1968) and the *Index to Plant Chromosome Numbers* (Goldblatt and Johnson 2003). The basal angiosperms (*sensu* Soltis and Soltis 2004) were excluded from this analysis because only three species (*Nymphaea odorata*, *N. alba* and *N. mexicana*) are represented from the combined taxa that make up this group and of these, only *N. odorata* ($2n$ = 84) has a published chromosome number (Hickman 1993).

We tested whether predictions can be made about the time between detection and widespread occurrence (defined here as present in 29 or more counties) for most alien taxa. The number of counties in which a taxon occurs was determined from the hierarchically defined geographical ranges provided in Hickman (1993) and Hrusa et al. (2002) and summarized in Schmid (1996). We recognize that counties are political boundaries and vary greatly in size; however, they provide the most useful measure of distribution. The total number of counties we report is greater than the 58 found in the state because of additional county divisions (e.g., "Northern San Bernardino Co.") and the Channel Islands. The following four range size categories were used: "a" = occurrence in 1–14 counties; "b" = occurrence in 15–28 counties; "c" = occurrence in 29–42 counties; and "d" = occurrence in 43–62 counties. Respective chi-square tests for each alien flora (Jepson 1925; Munz 1968; Hickman 1993; Hrusa et al. 2002) were performed between the actual and expected number of species in each range size.

SigmaStat Ver. 3.2 (SPSS Science, Chicago, IL) was used for all statistical analyses.

Results

Taxonomic Patterns

Only ten plant families account for nearly two-thirds of the non-native flora of California (Table 2). Some (Fabaceae, Poaceae, Brassicaceae, Caryophyllaceae, Chenopodiaceae) have significantly higher representation in the non-native flora of California than in its native flora (Table 2) while other families have significantly lower representation. Families with representation greater than 2% of the native flora but significantly fewer representatives in the non-native flora are the Scrophulariaceae, Polygonaceae, Liliaceae, and Cyperaceae.

Some families without representation in the native flora of California have provided some of its worst invaders, e.g., *Tamarix ramosissima* and *Eucalyptus globulus* (Table 3). Additionally, although a family may be represented in the native flora, some invaders are in genera for which there are no native species; for example, *Centaurea*, *Brassica*, *Sisymbrium*, *Ipomoea*, *Genista*, *Medicago*, *Avena*, and *Polypogon*. Some caution however, is advised in the use of family as a measure of relatedness; for example, the Tamaricaceae recently has been recognized as closely allied to the Frankeniaceae (APG 2003), which does have native representatives in California.

Geographic Origins

The geographic source of plant introductions versus time of introduction are shown in Table 4. The source of most introduced species prior to 1925 is Europe, Eurasia, and the eastern U.S. Although introductions increase from all geographic regions from 1925 to 1969, notable increases are present for Asia, Australia, Africa, South Africa, South America, and the southwestern United States, continuing through 2002 (Hrusa et al. 2002).

Habitat Characteristics

Seventy-nine percent of all of the non-native species in California occur in disturbed habitat. The most widespread species are those that occur in disturbed habitats, either commonly or uncommonly (Table 5).

Representation of all the families with the most non-natives decreases with increasing elevation. Only 41 taxa have a distribution that includes an elevation of 2500 m or higher. Taxa

TABLE 2. FAMILIES WITH THE LARGEST REPRESENTATION IN NON-NATIVE FLORA OF CALIFORNIA AS SUMMARIZED FROM HICKMAN (1993) AND HRUSA ET AL. (2002). A two-sided z test for significant differences between proportions was calculated for each family. The native geographic distribution of all families listed is "cosmopolitan". The Scrophulariaceae, Polygonaceae, and Caryophyllaceae are cosmopolitan but found primarily in the Northern Hemisphere.

Family	# Native taxa	% native flora	# non-native taxa	% non-native flora	Z-test value	P value
Asteraceae	913	18.8%	178	16.7%	1.80	0.072
Fabaceae	414	8.5%	117	11.0%	2.64	0.0082
Scrophulariaceae	321	6.6%	44	3.3%	5.44	<0.0001
Poaceae	287	5.9%	210	16.0%	9.51	<0.0001
Polygonacae	294	6.1%	30	2.3%	7.08	<0.0001
Liliaceae	263	5.4%	22	1.7%	7.70	<0.0001
Cyperaceae	202	4.2%	25	1.9%	4.86	<0.0001
Brassicaceae	272	5.6%	69	5.2%	0.58	0.5619
Caryophyllaceae	84	1.7%	42	3.2%	2.90	0.0037
Chenopodiaceae	73	1.5%	32	2.4%	1.98	0.0477

within the Poaceae and the Brassicaceae have the broadest distribution across elevational ranges (Table 6).

Polyploidy

The number of non-native polyploid taxa is higher than the non-native diploid taxa for both eudicots and monocots (Table 7). There is no correlation with the number of counties occupied and chromosome number (Tables 8 and 9).

Time Since Introduction and Spread

Fifty-three percent of the species recorded as present in California prior to 1925 currently occupy 43 or more counties compared to only 4.1% of introduced species listed in Hickman (1993) and 0.7% of those listed in Hrusa et al. (2002) (Table 8). Of those non-native species present since at least 1925 (185), 67.6% are present in 29 or more counties. Comparatively, of those species that were recorded between 1925 and 1968, only 37.0% are present in 29 or more counties.

All non-native species present in the 1925 Jepson are present in the 1993 Jepson. However, of 32 taxa present since at least 1925 that occur in only 1–14 counties, 12 (37.5%) occur in disturbed habitat, 7 (21.0%) occur in disturbed but uncommon habitat, 8 (25.0%) are habitat specific, and 5 (15.6%) are habitat specific and uncommon. Of the 145 taxa present since at least 1925 that occur in 43 or more counties, 118 (81.3%) occur in disturbed habitat, 6 (4.1%) occur in disturbed habitat but are uncommon, 18 (12.4%) are habitat specific, and 3 (2.1%) are habitat specific and uncommon.

DISCUSSION

The comparative analysis of the historical changes and current composition of California's non-native flora provides some interesting trends for a large, well-studied, and ecologically diverse region.

Taxonomic Pattern

A few families have statistically higher levels of frequency in the non-native flora than in the native flora. Of particular note are the Fabaceae, Poaceae, Caryophyllaceae, and Chenopodiaceae. The Poaceae, a large and cosmopolitan family, contains some of the world's worst invaders (Mack et al. 2000).

A taxon previously absent from or with a poor representation in the state is likely to contain at least some invaders as most clearly illustrated by California's invasive flora from the Myrtaceae (*Eucalyptus globulus*), Tamaricaceae (*Tamarix ramosissima*, *T. chinensis*), *Brassica*, *Avena*, *Genista*, and others. Thus native representation should be considered in the prioritization of invasive plant species for control efforts.

Geographic Origins

Humans are now the most important vector for plant dispersal (Mack and Lonsdale 2001). The geographic origins of non-native species in California reflect the state's settlement history. Immigrants to California were initially of European/Eurasian origin and are now primarily from Latin America and Asia (U.S. Census Bureau 1990). Although the percentage of foreign-born residents of California has remained at about 24%, the population of California has grown from 1.5 million in 1900 to over 35 million in 2002. The specific distribution of California's foreign-born residents in 1900 is not available, but 75% of the foreign-born residents in the entire U.S. were from Europe (including the United Kingdom and Scandinavia), 11% from Eastern Europe, 1.2% from Asia, 1.3% Latin America, and the remainder miscellaneous. In contrast, in 1990, 60.7% of the 6.5 million

TABLE 3. GENERA WITH THE LARGEST NUMBER OF NON-NATIVE Species (≥5) IN CALIFORNIA AS SUMMARIZED FROM HICKMAN (1993) AND HRUSA ET AL. (2002). *Notable increases since Hickman 1993

Family	Genus	# non-native spp.	#native spp.	Family native ?	Family native to
Amaranthaceae	*Amaranthus*	9	7	Y	Tropics, subtrop.
Asteraceae	*Centaurea*	13	0	Y	Cosmopolitan
Brassicaceae	*Brassica*	6	0	Y	Cosmopolitan
	Lepidium	6	15		
	Sisymbrium	6	0		
Caryophyllaceae	*Silene*	7	23	Y	Widesprd; N. hemis
Chenopodiaceae	*Atriplex*	8	31	Y	Cosmopolitan
	Chenopodium	15	13		
Convolvulaceae	*Ipomea*	8*	0	Y	Warm temp-trop.
Euphorbiaceae	*Euphorbia*	17*	7	Y	Cosmopolitan
Fabaceae	*Acacia*	11	1	Y	Cosmopolitan
	Genista	6	0		
	Lathyrus	8	17		
	Medicago	7	0		
	Trifolium	25*	32		
	Vicia	14	4		
Geraniaceae	*Erodium*	6	2	Y	Temp., trop
	Geranium	13	5		
	Pelargonium	9	0		
Myrtaceae	*Eucalyptus*	9	0	N	Trop., sub-trop., S. hemis.
Onagraceae	*Oenothera*	6	10	Y	Cosmopolitan, esp. NA
Oxalidaceae	*Oxalis*	8	4	Y	Esp. Temp.
Plantaginaceae	*Plantago*	8	7	Y	Cosmopolitan; esp. temp.
Polygonaceae	*Polygonum*	16	18	Y	Cosmopolitan; esp. n. temp.
	Rumex	9	7		
Ranunculaceae	*Ranunculus*	9	22	Y	Cosmopolitan; esp. N. temp.
Rubiaceae	*Galium*	7	40	Y	Cosmopolitan; esp. Trop.
Scrophulariaceae	*Linaria*	7	1	Y	Cosmopolitan
	Verbascum	5	0		
	Veronica	9	7		
Solanceae	*Physalis*	5	4	Y	Cosmopolitan; esp. Trop.
	Solanum	16	6		
Tamaricaceae	*Tamarix*	5	0	N	Eurasia
Cyperaceae	*Cyperus*	11*	11	Y	Cosmopolitan; esp. Temp.
Poaceae	*Agrositis*	6	15	Y	Cosmopolitan
	Avena	5	0		
	Bromus	14	9		
	Eragrostis	6	7		
	Phalaris	7	4		
	Poa	8	25		
	Polypogon	6	0		
	Setaria	5	1		

immigrants in California were from Latin America, 27.5% from Asia, 4.7% from the Middle East, 4.0% from Europe and the former USSR, 2.2% British (including Canada, Australia, and New Zealand), and 0.8% from Africa (U.S. Census Bureau 1990). The trends that we observed in the geographic origins of California's non-native plant immigrants track the trends just described for human immigration, namely that Europe and Eurasia were the primary sources of the initial immigrant flora with Latin America and Asia playing an increasingly role over time (Table 4). Our observation that plant introductions are likely linked to human immigration is consistent with recent work that cites that the cultural utilization of plants can mimic the demographic expansion of an invader; a phenomenon illustrated by the European settlement of California grasslands from 1770 through 1880 and the concomitant spread of *Avena* and *Bromus* species (Kowarik 2003; Mack 2003).

Habitat Characteristics

There are a number of difficulties interpreting the "disturbed habitat" category. We use "disturbed habitat" as a general term to encompass the variety of habitat conditions or distributions used in Hickman (1993) and include any taxon that occurs either partly or wholly in

TABLE 4. GEOGRAPHIC SOURCE OF PLANT INTRODUCTIONS VERSUS YEARS SINCE FIRST APPEARANCE IN A FLORA. Place of origin listed as provided by Jepson (1925), Munz and Keck (1958), Munz (1969), Hickman (1993), and Hrusa et al. (2002).

Year intro.	Africa	Asia	Austral Asia	Australia	East/Cen. US	Eurasia	Europe	Mexico	New Zealand	South Africa	South America	Southwest US
≥4	6	26	1	7	26	26	49	4	2	22	31	5
≥10	5	13	1	17	19	18	69	1	5	16	15	1
≥35	19	42	5	16	44	82	237	8	3	27	71	20
≥78	3	2	3	5	21	46	160	2	0	6	17	4

Year intro.	Canary Islands	Caribbean	Cultivated	Old World	Tropics	Unknown	Hybrid	S. Pacific Islands	Northern Hemisphere
≥4	4	0	2	5	5	71	8	0	5
≥10	7	2	1	1	1	1	0	0	0
≥35	8	0	0	5	2	3	3	1	0
≥78	0	1	0	3	1	0	0	0	0

human-altered habitats. Taxa that occur in disturbed habitat, as defined here, are more likely to spread throughout the state than those with more specialized habitat requirements. Our data (Table 5), consistent with the following conclusions of Dark (2004), indicate that this is particularly true at low elevations. Dark (2004) compared 78 invasive, non-native species with 1097 non-invasive, non-native species in California and found a higher concentration of invasive, non-native species in coastal regions. She also found the number of non-native species in California was significantly lower at higher elevations, significantly increased with increasing road density, and decreased as native plant species richness increased. Her results are consistent with the ideas that roads provide an opportunity for colonization and that invasions are associated with anthropogenic disturbance (Hobbs and Huenneke 1992; Sax 2002).

The vacant niche hypothesis as used by Simberloff (1981) predicts that unoccupied habitats are vulnerable to invasion. For example, resource availability and native species diversity are lower in California's alpine communities (Holland and Keil 1995; Keeley et al. 2003; D'Antonio et al. 2004). Keeley et al. (2003) found that, although the number of non-native species decreases dramatically at elevations greater than 1800 m in the Sierra Nevada, native species also show a steep decline. We found only 41 non-native taxa with a distribution that includes an elevation of 2500 m or higher (Table 6), but of these, the Poaceae, Asteraceae, and Brassicaceae have high representation. The Coast Ranges and Sierra Nevada foothills have higher invasive species diversity; however they also have higher native species diversity (Keeley et al. 2003).

The disruption of fire regimes is documented as increasing the occurrence of non-native species, particularly in California's Coast Ranges and foothills where high fire frequency has contributed to the conversion of chaparral and woodland communities to annual grasslands dominated by non-native species (Keeley 2001). The high occurrence of non-native members of the Poaceae in coastal and foothill habitats suggests it would be prudent to implement early control of any member of this family, particularly those that occur in habitat that has been disturbed in any manner.

Polyploidy

Taxa of polyploid origin are overwhelmingly represented in the non-native species of California; of the 791 taxa for which we had chromosome numbers, 62.5% of eudicots, and 91.7% of monocots had values of $2n \geq 14$ (Table 7).

TABLE 5. GENERAL HABITAT TYPE AND GEOGRAPHIC DISTRIBUTION OF RECORDED NON-NATIVE TAXA IN CALIFORNIA AS SUMMARIZED FROM HICKMAN (1993) AND HRUSA ET AL. (2002). Disturbed = Occurs in disturbed areas; Disturbed Uncommon = occurs in disturbed areas but uncommon; Habitat Specific = occurs in specific habitats; and Habitat Specific, Uncommon = occurs in specific habitats and uncommon. For some species, if the information provided was ambiguous or not provided, it was not included.

Occurrence	Disturbed	Disturbed uncommon	Habitat specific	Habitat specific uncommon
1–14 counties	126	129	40	69
15–28 counties	138	69	50	13
29–42 counties	95	23	25	7
43–62 counties	204	41	31	6
	564	262	146	95
Percent of total:	52.8%	24.5%	13.7%	8.9%

TABLE 6. ELEVATIONAL DISTRIBUTION OF SPECIES IN THE MOST COMMON NON-NATIVE FAMILIES IN CALIFORNIA AS SUMMARIZED FROM HICKMAN (1993) AND HRUSA ET AL. (2002).

	≤100 m	≤500 m	≤1000 m	≤2000 m	≤3000 m
Apiaceae	1	3	11	5	0
Asteraceae	18	70	35	42	9
Brassicaceae	6	29	12	24	7
Caryophyllaceae	2	14	8	14	4
Fabaceae	18	52	23	20	2
Poaceae	33	68	40	54	16
Scrophulariaceae	14	11	9	7	3

However, there is no conclusive and comparative measure of polyploidy that we can use to determine whether this fraction represents an over-representation. In addition to Grant's (1981) estimates, Stebbins (1971) estimated approximately 50% of all angiosperms were polyploids, but based on fossil evidence, Masterson (1994) estimated polyploidy as high as 80%. Over time, we found no correlation between habitat type and chromosome number (Table 9), contrary to the prediction that polyploid taxa should have a wider distribution than diploid taxa (Stebbins 1942, 1971).

Time Since Introduction and Spread

Based on the data presented in Table 8 and assuming no additional introductions of new species and that those recently introduced species spread at rates roughly similar to those introduced earlier, in approximately 40 yrs, there will be 403 non-native species present in 29 or more counties; in about 80 yrs 530 such species will be present in 29 or more counties; and in approximately 100 yrs, 737 introduced species will be present in 29 or more counties. A few caveats should be noted regarding these predictions however; many areas of California are less populated and comparatively less disturbed than others, so this pattern may be an artifact of human population dispersal. Additionally, many species that may have been previously widely distributed may have been collected within the last two decades because of an increased interest in non-native species.

Our data demonstrate for California that after at least 80 yrs, over 50% of all plant species that have been introduced and detected enough to be listed in the flora ("casual reproducers" as defined by Richardson et al. 2000) have become widespread, and of these, 81% occur in disturbed habitat. However, some qualifications

TABLE 7. DISTRIBUTION OF CHROMOSOME NUMBERS FOR RECORDED NON-NATIVE SPECIES IN CALIFORNIA. Total # of species for which there is chromosome number = 791. See methods for sources of data. *Calculated as percentage of those eudicots/monocots for which chromosome numbers are known.

	Eudicots	% of eudicots*	Monocots	% of monocots*
$2n \leq 12$	28	4.5%	14	8.3%
$2n = 14–18$	216	3.5%	33	19.5%
$2n \geq 19$	367	59.0%	122	72.2%
Total	622		169	

TABLE 8. RANGE OF OCCURRENCE OF NON-NATIVES COMPARED WITH YEARS SINCE FIRST APPEARANCE IN A FLORA. Chi-square value = 647.748, df = 6, $P \leq 0.001$. Chi-square values calculated as $\chi^2 = \sum[(O - E)^2/E]$. O is the observed frequency of individuals per cell, E is the expected frequency of individuals per cell, and the sum is over all the cells in the contingency table. Expected frequencies were calculated from a 4×4 contingency table in which the rows were the county categories (a,b,c, and d) and the columns, the time that these species first occurred; e.g., the first cell contained the number of species first reported in Jepson that occur in 1–14 counties, etc.

	First recorded in:			
	Jepson (1925)	Munz (1968)	Hickman (1993)	Hrusa et al. (2002)
Occurrence				
1–14 counties				
actual	32 or 11.7%	197 or 33.0%	132 or 68.0%	301 or 99%
expected	132	289	91	147
15–28 counties				
actual	57 or 21.0%	176 or 29.5%	36 or 18.6%	1 or 0.3%
expected	54	118	37	60
29–42 counties				
actual	40 or 14.6%	98 or 16.4%	13 or 6.7%	0 or 0
expected	30	66	20	33
43–62 counties				
actual	145 or 53.0%	126 or 21.0%	8 or 4.1%	2 or 0.7%
expected	56	122	38	62

should be considered in the data interpretation. Some non-native taxa recorded prior to 1925 may have been noticed due to their aggressiveness. Conversely, some species recorded after 1925 may have had earlier introductions but remained undetected. Regardless, the data reflect a strong relationship between time since introduction and spread. Because the introductions from Asia and Africa have recently increased, and many genera and families may be novel to California, particular caution should be noted for these taxa.

CONCLUSIONS

Our results are consistent with the observation that despite the evidence for global homogenization of ecosystems, regional diversity is increasing in the area we call California (Sax and Gaines 2002). Over the last hundred years, it appears that the total number of California plant species has been increasing. Although somewhat equivocal, based on published floras, it appears that not one of the alien plant taxa recorded prior to 1925 has gone extinct in the state. It is clear that

TABLE 9. CHROMOSOME NUMBER, GEOGRAPHIC DISTRIBUTION, AND YEARS SINCE FIRST APPEARANCE IN A FLORA FOR 791 TAXA FOR WHICH CHROMOSOME NUMBERS WERE AVAILABLE. See methods for data sources. Linear regression for number of counties vs. chromosome number does not support a relationship between these two variables (adjusted $R^2 = 0.0081$, $P = 0.009$).

	First occurrence in:			
Geographic Distribution	Hrusa et al. (2002)	Hickman (1993)	Munz (1968)	Jepson (1925)
Chromosome number ($2n$) $\leq$ 12				
1–14 counties	16	2	8	2
15–28 counties	0	1	8	1
29–42 counties	0	0	2	1
43–62 counties	1	0	5	6
Total	17	3	23	10
Chromosome number ($2n$) = 14–18				
1–14 counties	16	11	34	8
15–28 counties	0	5	26	16
29–42 counties	0	2	20	10
43–62 counties	0	1	37	26
Total	16	19	117	60
Chromosome number ($2n$) $\geq$ 20				
1–14 counties	14	39	74	15
15–28 counties	0	9	84	32
29–42 counties	0	6	49	22
43–62 counties	1	5	66	100
Total	15	59	273	169

many local areas of California have undergone tremendous changes in the composition of the predominant plant community. Thus, we caution that at smaller regional scales (i.e., within most respective coastal, valley, montane, and desert ecosystems of California) the data to determine changes in diversity due to non-natives species remain to be collected.

Hobbs and Humphries (1995) postulated three reasons for the time-lags in plant invasions: genotypic adaptations; cyclical disturbance or a combination of environmental conditions; and the observance that species, with exponential growth, are not observed until the population reaches a critical size. In addition, Ellstrand and Schierenbeck (2000) provided a number of examples to support the evolution of invasiveness resulting from multiple introductions and subsequent inter- or infra-specific hybridization. The data we present here provide a presentation of the delay present in the spread of many of the non-native plant species in California and establish that a combination of human disturbance and introduction patterns as key to the history of California plant invasions. Whether this delay is due to the spread of nascent foci, detection ability, natural selection, or environmental stochasticity may never be answered (Mack et al. 2000). Regardless, over time, more than 50% of all alien taxa documented in the California flora have become widespread in California.

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ENVIRONMENTAL AND ECOLOGICAL EFFECTS ON SIZE CLASS DISTRIBUTIONS OF FOXTAIL PINE (*PINUS BALFOURIANA*, PINACEAE) IN THE KLAMATH MOUNTAINS, CALIFORNIA

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ABSTRACT

Variation in size class distributions along elevation gradients can indicate localized spatial expansion by tree populations inhabiting mountaintops. We searched for this pattern in northern foxtail pine (*Pinus balfouriana* Grev. & Balf. ssp. *balfouriana*) stands located in the Klamath Mountains of northern California. Data from 32 belt-transects placed within 16 foxtail pine stands were used to test the hypothesis that this species is expanding downslope locally. Nonmetric multidimensional scaling (NMS) illustrated that size class distributions could be grouped into four types: (1) those at low elevations on north and east aspects; (2) those at low elevations on south and west aspects; (3) those at high elevations on north and east aspects; (4) those at high elevations on south and west aspects. Low elevation transects had greater abundances of small trees, while high elevation transects had greater abundances of large trees. We interpreted this pattern as support for the hypothesis that foxtail pine is locally expanding downslope in the Klamath Mountains. Further analyses showed that NMS dimensions were correlated with estimates of tree density, species diversity, the importance of shade-tolerant conifers, and boulder cover. Moreover, the importance of shade-tolerant conifers was related to aspect, substrate type, boulder cover, and interactions among these variables. The pattern of those correlations suggests that several ecological and environmental factors affect the ability of foxtail pine to expand downslope through alleviation or alteration of competitive interactions. Those results provide an ecological context for climate-mediated range expansions and retractions in northern foxtail pine.

Key Words: foxtail pine, Klamath Mountains, microsites, *Pinus balfouriana*, size class distribution, spatial expansion.

Spatial patterns of dispersion are scale-dependent in forest trees (Szwagrzyk and Czerwczak 1993; Ribbens et al. 1994; Nathan and Muller-Landau 2000; Hubbell 2001). At small spatial scales, dispersion patterns typically differ among size classes, with seedlings and saplings being clumped and adult trees randomly dispersed throughout stands (Platt et al. 1988; Szwagrzyk and Czerwczak 1993; Nathan and Muller-Landau 2000). This pattern is often attributed to dispersal limitations, competition, or the outcome of adaptive life history strategies such as colonization-competition tradeoffs (Ribbens et al. 1994; Clark et al. 2004; McEuen and Curran 2004).

At large spatial scales, adult trees tend to be found on topographically stable landforms, while seedlings and saplings are more common in areas prone to disturbance or resource limitation (Basnet 1992; Desta et al. 2004; Pollmann and Veblen 2004). Patterns such as these have been interpreted in various ways (Fox and Gurevitch 2000). When assemblages are structured along elevation gradients, the typical interpretation of those patterns is one of localized upslope or downslope expansion (Pollmann and Veblen 2004).

The structure and composition of species assemblages can have large effects on those patterns (Desta et al. 2004). Moreover, moisture availability as a function of aspect is often found to influence the composition and structure of forest tree assemblages (Rundel et al. 1988; Sawyer and Thornburgh 1988; Urban et al. 2000). This is especially true in geographic areas prone to summer drought (Major 1988; Sawyer and Thornburgh 1988). Here, we examine the influence of aspect, elevation, and the distribution of co-occurring conifers on the size class distributions of foxtail pine (*Pinus balfouriana* Grev. & Balf.) stands to test the hypothesis that this species is expanding downslope from mountaintop populations located in the Klamath Mountains.

The Klamath Mountains are a geologically complex system of mountain ranges located in northern California and southern Oregon (Fig. 1). Forest types are diverse and represent mixtures of Cascadian and Sierran elements (Whittaker 1960). These forests likely originated in their modern form no longer than 10,000 to 15,000 yr ago (Sawyer and Thornburgh 1988; Wanket 2002; Sawyer 2006). Regional conifer

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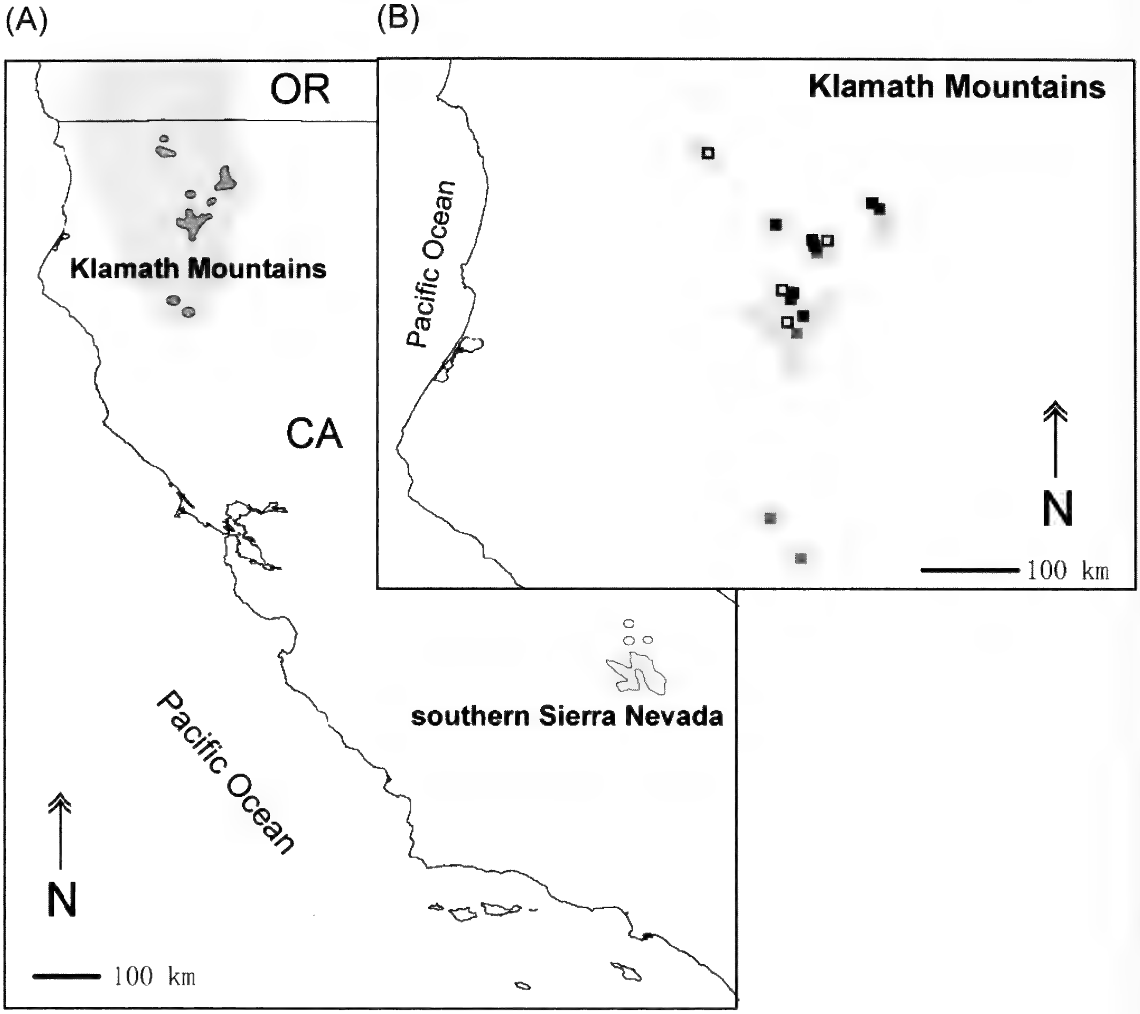

FIG. 1. Distribution of foxtail pine (*Pinus balfouriana* Grev. & Balf.) in California. (A). The distribution of this species in California is disjunct. The extent of the Klamath Mountains is shown in light grey, while the distribution of foxtail pine is shown in dark grey. (B). The distribution of foxtail pine in the Klamath Mountains. Sampled stands are indicated with squares that are color-coded by aspect class (black = north; dark grey = east; light grey = south; white = west).

diversity is high, due in part, to a suite of rare and endemic species.

Northern foxtail pine (*P. balfouriana* ssp. *balfouriana*) is one such conifer. Previous research has shown that this species is largely restricted to localities on ultramafic substrates or those with abundant suitable microsites (Eckert and Sawyer 2002). Foxtail pine stands on ultramafic substrates have reduced densities, basal areas, and frequencies of shade-tolerant competitors such as *Abies magnifica* A. Murr. ssp. *shastensis* Lemmon and *Tsuga mertensiana* (Bong.) Carr., while stands with abundant microsites (i.e., abundant spatially isolated patches of soil amongst inhabitable areas) have increased species diversities (Eckert 2006a). Those patterns of habitat heterogeneity were offered as the primary mechanism of foxtail pine persistence in the conifer-rich Klamath Mountains through competition avoidance within a variable habitat.

Several ecological and dendrochronological studies of foxtail pine stands in the southern Sierra Nevada indicate that numerous rounds of downslope and upslope expansion have likely occurred in the past as a function of regional climate changes and topographic effects on local climates (Ryerson 1983; Lloyd 1997; Lloyd and Graumlich 1997; Millar et al. 2004; Bunn et al. 2005). Similar studies for the populations of foxtail pine located in the Klamath Mountains are lacking. Patterns of climate-induced tree mortality and population expansions and retractions may differ between the southern Sierra Nevada and the Klamath Mountains, especially given the observed differences in

environmental, climatic, and ecological conditions (Rundel et al. 1988; Sawyer and Thornburgh 1988). Specifically, the ecological context of foxtail pine drastically differs between those regions (Eckert and Sawyer 2002).

In the Klamath Mountains, ecotones are sharp and downslope movement would involve colonization within a dense matrix of shade-tolerant competitors. When coupled with the observations of Eckert (2006a), these patterns suggest that the distribution of competing conifer species, which is in turn a function of habitat heterogeneity (i.e., ultramafic soils and microsites), affects the ability of foxtail pine to expand downslope. Therefore, the influence of aspect, substrate type, and boulder cover on the ability of foxtail pine to expand downslope may be acting through alteration or alleviation of competitive interactions.

The diverse subalpine forests of the Klamath Mountains offer a unique system with which to analyze the effects of topography and species interactions on size class distributions of a locally dominant species. We address this topic for foxtail pine using a four-step approach. First, we use ordination to address the question of whether or not foxtail pine is expanding downslope in the Klamath Mountains as a function of aspect. Second, we investigate the correlation of ecological and environmental variables with observed multidimensional patterns. Third, we test the hypothesis that substrate type, aspect, and microsite availability affect the local dominance of shade-tolerant conifers. Lastly, our results are extended to a generalized hypothesis of how differences in habitat conditions may affect the ability of foxtail pine to expand downslope as a function of the local dominance of shade-tolerant competitors and relate this hypothesis to the further need for climate-based analyses.

Materials and Methods

Study Area, Stand Selection, and Sampling

Study Area. In northern California, the Klamath Mountains are a geologically complex mosaic of mountain ranges characterized by diverse substrates, climates, and vegetation types (Major 1988; Sawyer and Thornburgh 1988; Safford et al. 2005). Substrate types range from igneous to ultramafic, with most ultramafic substrates being located in the eastern portion of the region. Climate conforms to a modified Mediterranean type characterized by dry summers and wet winters, with thunderstorms developing during the late summer. Those climate patterns form a sharp wet-to-dry moisture gradient across the west-east axis of the region (Major 1988). Vegetation types range from lowland chaparral to subalpine conifer forests with high levels of plant endemism and diversity.

Stand Selection and Sampling. We identified 16 stands of foxtail pine that were equally distributed among four aspect classes. Selected stands represent a subset of those sampled by Eckert (2006a), who used a stratified random sampling approach for stand selection. Aspect classes were based on the four cardinal directions (north: 315–45°; east: 45–135°; south: 135–225°; west: 225–315°). Within each stand, we established two 200-m long by 50-m wide belt-transects located at the lowest and highest local elevations. The low elevation belt-transects were located at the lowest elevation that still had foxtail pine in densities greater than 50 trees ha^{-1}. At densities less than 50 trees ha^{-1}, foxtail pine is not the dominant tree species (Eckert and Sawyer 2002; Eckert 2006a).

In each belt-transect, the density (trees ha^{-1}) and basal area (m^2 ha^{-1}) of trees greater than 1.37 m in height were determined using the point-centered-quarter (PCQ) method with 10 randomly spaced points (n = 40 trees) and the unbiased estimator of Pollard (1971). Density and basal area were transformed into an index of importance (I) for each species using the following formula:

$$I_i = \left[\frac{D_i}{D} + \frac{BA_i}{BA}\right] \Big/ 2$$

where, D_i is the density of species i, BA_i is the basal area for species i, D is the total stand density, and BA is the total stand basal area. Species richness (SR), diversity (Shannon-Wiener information statistic [H']), and equitability (E) were determined from PCQ data using the number of species sampled (species richness) and their relative frequencies (p_i) in the sample (diversity: $H' = -\sum_{i=1}^{k} p_i \ln p_i$; equitability: $E = H'/\ln SR$).

The diameter at breast height (DBH) was measured for a sample of 75 foxtail pine trees greater than 1.37 m in height. Trees were sampled along a wandering line transect placed within each belt-transect following the protocol outlined by Bonham (1989). The position of each tree was mapped using a GARMIN eTREX Venture GPS receiver (GARMIN International, Olathe, KS), and the mean of their elevation measurements was used as the absolute elevation (m) for each belt-transect. Trees were subsequently classified into one of 10 non-overlapping size classes based on DBH (≤25 cm, 25.01–46 cm, 46.01–65 cm, 65.01–84 cm, 84.01–102 cm, 102.01–119 cm, 119.01–136 cm, 136.01–153 cm, 153.01–169 cm, ≥169.01 cm), which approximately correspond to 100-year age classes (Eckert and Sawyer 2002). We also estimated boulder cover (%) within each belt-transect using four one-m^2 plots. The cover of boulders in each of those one-m^2 plots was visually estimated using a grid with 16 sections. Boulders were defined as rock fragments greater

than 50 cm in diameter. The cover of boulders was equated with microsite availability (see Eckert 2006a).

Statistical Hypothesis Testing

The effects of aspect, elevation, and substrate type on ecological and environmental characteristics of stands were investigated with standard parametric statistical procedures (e.g., two-sample and paired t-tests, analysis of variance [ANOVA], and analysis of covariance [ANCOVA]) using a critical value of $P = 0.05$. All t-tests were two-tailed. All ANOVAs with significant effects were followed by Tukey-Kramer multiple comparison tests to detect differences among treatment means. Data from different transects in the same stand were grouped prior to statistical testing when the hypothesis being tested concerned differences at the stand level. Prior to performing these tests, the assumptions of normality and equal variances were verified using standard procedures (Zar 1999). We log-transformed data when necessary to meet those requirements. All statistical analyses were conducted with NCSS unless otherwise noted (Hintze 2001).

We compared size class distributions among transects using a three-step approach. First, we identified transects with similar size class distributions using ordination. Multivariate distances were constructed among transects (n = 32) using unweighted Euclidean dissimilarities based on size class distributions and subjected to nonmetric multidimensional scaling (NMS). This technique is robust to common statistical problems associated with ordination procedures (Kruskal 1964; Fasham 1977; Kenkel and Orlóci 1986; Minchin 1987). The solution from classical multidimensional scaling (CMS) was used as the starting configuration for a maximum of 100 iterative starts in NMS (Torgeson 1965). This was done to minimize the likelihood of identifying local optima. We chose to limit our examination to three dimensions and gauged the fit of the NMS distances to the original dissimilarity matrix with a Shepard plot.

Second, we determined the statistical significance of groups using analysis of similarity (ANOSIM; Clarke 1993). This method constructs a test statistic (R) from the mean ranks of dissimilarity values within versus among categories and tests this statistic by comparison to a null distribution derived from permutations of category labels among samples. Categories correspond to NMS-defined groups, while samples are equated with transects. We performed tests for all groups considered at once and all pairwise two-way comparisons using a Bonferroni correction, so as to approximate standard multiple comparison tests (Zar 1999).

TABLE 1. AVERAGE ENVIRONMENTAL AND ECOLOGICAL CHARACTERISTICS OF 16 FOXTAIL PINE STANDS SAMPLED FROM THE KLAMATH MOUNTAINS GROUPED BY ASPECT CLASS (N = 4 STANDS IN EACH CLASS). Standard errors of the mean are located below each average in parentheses. BA = basal area, BC = boulder cover, D = density, E = equitability index, H' = Shannon-Wiener diversity index, PIBA I = *Pinus balfouriana* importance index, SR = species richness.

Aspect	Area (ha)	Elevation (m)	Slope (%)	Stands on Serpentine	BC (%)	D (trees/ha)	BA (m²/ha)	PIBA I	SR	H'	E
North	31.45	2159.00	23.64	3	42.32	220.25	26.76	0.57	5.50	1.11	0.72
	(6.84)	(80.50)	(6.80)	—	(9.11)	(57.38)	(4.10)	(0.14)	(0.50)	(0.23)	(0.06)
East	20.03	2323.75	43.30	2	33.17	188.25	24.65	0.53	5.00	1.11	0.72
	(4.64)	(67.61)	(3.48)	—	(14.05)	(45.46)	(5.17)	(0.13)	(1.41)	(0.29)	(0.09)
South	21.25	2300.75	33.22	2	30.22	176.25	26.89	0.59	4.25	0.97	0.73
	(7.14)	(27.45)	(2.30)	—	(4.67)	(46.49)	(7.30)	(0.04)	(0.48)	(0.04)	(0.07)
West	15.25	2176.25	28.58	2	31.14	137.75	11.40	0.60	4.00	0.99	0.68
	(2.71)	(39.68)	(7.16)	—	(6.55)	(24.15)	(3.33)	(0.09)	(0.00)	(0.15)	(0.08)

TABLE 2. EXPLORATORY ANALYSES (TWO-SAMPLE AND PAIRED T-TESTS AND ANOVAS) FOR THE EFFECTS OF ELEVATION (DF = 30), SUBSTRATE TYPE (DF = 14), AND ASPECT (DF_1 = 3, DF_2 = 12) ON ECOLOGICAL CHARACTERISTICS FROM 32 BELT-TRANSECTS LOCATED IN 16 FOXTAIL PINE STANDS DISTRIBUTED THROUGHOUT THE KLAMATH MOUNTAINS OF CALIFORNIA. Significant effects in the ANOVAs were further investigated using Tukey-Kramer multiple comparison tests. Effects refer to the relative magnitudes of the means for samples used in the described statistical tests. BA = stand basal area (m^2/ha), D = stand density (trees/ha), E = east, H' = Shannon-Wiener information statistic, High = high elevation transect, I_{PIBA} = foxtail pine importance, Low = low elevation transect, N = north, nu = non-ultramafic substrate, SHADE = summed importance of shade-tolerant conifers, S = south, SR = species richness, u = ultramafic substrate, W = west.

	Elevation (paired)			Substrate (two-sample)			Aspect		
	t	P	Effect	t	P	Effect	F	P	Effect
SR	2.865	0.008	High < Low	1.000	0.334	nu = u	2.465	0.112	W = S = E = N
D	0.963	0.343	High = Low	1.334	0.203	nu = u	1.010	0.422	W = S = E = N
BA	1.269	0.214	High = Low	0.278	0.785	nu = u	4.468	0.025	W < S, E, N
I_{PIBA}	2.535	0.017	High > Low	2.179	0.047	nu < u	0.262	0.851	W = S = E = N
SHADE	2.316	0.028	High < Low	2.596	0.021	nu > u	0.857	0.489	W = S = E = N
H'	3.074	0.004	High < Low	0.875	0.396	nu = u	1.733	0.213	W = S = E = N

Analyses were performed using the VEGAN package encapsulated in the R environment and 10,000 permutations (Ihaka and Gentleman 1996; Oksanen et al. 2005).

Lastly, simple linear regression models were used to examine the relationships among NMS dimensions, abundances of trees within each size class, and several ecological variables (i.e., H', species richness, importance index of foxtail pine, summed importance indices of shade-tolerant conifers). Shade-tolerant conifers were defined to be *Abies concolor* (Gordon & Glend.) Lindley, *A. magnifica* ssp. *shastensis*, and *Tsuga mertensiana*. We chose to use separate linear regression models, rather than multiple regression models, to avoid problems associated with multicollinearity (Zar 1999).

RESULTS

Ecological Characteristics of Transects

A total of 32 transects were sampled from 16 stands located throughout the Klamath Mountains (Table 1). Absolute measures of elevation ranged from 1910 m to 2422 m for low elevation transects and from 1956 m to 2527 m for high elevation transects. On average, high and low elevation transects were separated from one another by 95 m ($\pm$47 m) in elevation and were within one km of each other. Aspect had no effect on elevation (ANOVA: $F_{3,12}$ = 2.612, P = 0.099) or boulder cover (ANOVA: $F_{3,12}$ = 1.493, P = 0.266). Substrate type was equally frequent among aspect classes and had no effect on elevation (two-sample t-test: t = 1.373, df = 14, P = 0.191) or boulder cover (two-sample t-test: t = 1.396, df = 14, P = 0.184).

Elevation, substrate type, and aspect differentially affected stand structure and composition (Table 2). The importance of foxtail pine increased with elevation, while species richness, the importance of shade-tolerant conifers, and H' decreased with elevation. Substrate type affected the importance values of foxtail pine and shade-tolerant conifers differently. Foxtail pine importance was greater on ultramafic substrates, while the importance of shade-tolerant conifers was greater on non-ultramafic substrates. Aspect had no effect on most measures of stand structure and composition. However, the basal areas of stands on western aspects were significantly smaller than stands on southern, northern, and eastern aspects.

Substrate type, aspect, and their interaction significantly affected the summed importance indices of shade-tolerant conifers once the effects of elevation and boulder cover were removed (Table 3). Separate ANCOVAs for each shade-tolerant conifer yielded the same result (not shown).

TABLE 3. ANCOVA FOR EFFECTS OF SUBSTRATE TYPE AND ASPECT ON THE SUMMED IMPORTANCE INDICES OF SHADE-TOLERANT CONIFERS WITH ELEVATION (M) AND BOULDER COVER (%) AS COVARIATES.

Factor	df_1	df_2	F	P
Substrate type	1	14	11.09	0.005
Aspect	3	12	5.00	0.015
Substrate type × Aspect	3	12	6.27	0.008
Elevation (covariate)	1	14	7.65	0.015
Boulder cover (covariate)	1	14	8.24	0.012

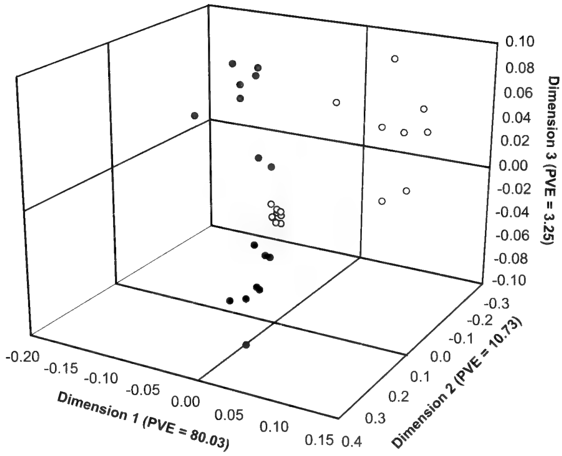

FIG. 2. Results of NMS based on unweighted Euclidean dissimilarities among size class distributions for 16 stands of foxtail pine located in the Klamath Mountains of northern California. The first three dimensions are plotted along with the percent variance explained (PVE) by the dominant eigenvalue for each dimension using the metric solution determined with CMS. Four potential groups are identified based on aspect and elevation — (1) low elevation with north and east aspects (black); (2) low elevation with south and west aspects (light grey); (3) high elevation with north and east aspects (white); (4) high elevation with south and west aspects (dark grey).

NMS Ordination

NMS Results. Ordination using NMS revealed four potential groups of transects defined by aspect and elevation (Fig. 2). Substrate type did not aid with defining these groups. Groups one and three were composed of transects located on north and east aspects at either low or high elevations, respectively. Groups two and four illustrated a similar pattern for transects on south and west transects. Inspection of stress and Shepard plots showed that our three dimensional representation of the original 10 dimensional space resulted in moderate distortion (stress = 0.026) and that transformation of the original dissimilarity matrix did not differentially distort dissimilarities of large magnitude. Adding additional dimensions (i.e., fourth, fifth, etc.) to the NMS analyses did not drastically reduce distortion. Furthermore, the dominant eigenvalues for each of the three dimensions in CMS solution, which was only used as a starting point for NMS, accounted for over 90% of the variation within the data.

Significance of NMS-Defined Groups. Differences among NMS groups were significant (ANOSIM: $R = 0.921$, $P < 0.001$). Alternatively, grouping transects by substrate type was not significant (ANOSIM: $R = 0.052$, $P = 0.365$). All possible pairwise comparisons across the four NMS groups showed that each group was statistically different from every other group ($n = 6$ pairwise comparisons, ANOSIM: $R > 0.85$, $P < 0.001$). In general, the largest differences were observed between groups differing in elevation. This is apparent in the shape of the average size class distributions for each group (Fig. 3). Transects at lower elevations had reverse J-shaped distributions (Fig. 3A, B), while transects at higher elevations, regardless of aspect, had multimodal distributions skewed towards larger trees (Fig. 3C, D).

Size Class and Ecological Correlates of NMS Dimensions

NMS dimensions were differentially correlated with the abundance of foxtail pine in each size class. Dimension one was positively correlated with size classes one ($r = 0.99$) and two ($r = 0.88$) and negatively correlated with size classes four through 10 ($-0.84 < r < -0.45$). The opposite trend was found for dimensions two and three, which were positively correlated with larger trees ($0.29 < r < 0.77$). These correlations indicated that the differences among NMS-defined groups were largely due to the greater abundances of smaller trees in low elevation transects and greater abundances of larger trees in high elevation transects. The effects of aspect were not as strong, but transects on southern and western exposures had increased abundances of large trees.

Several ecological variables were correlated with NMS dimensions. Dimension one was positively correlated with total density of trees ($r = 0.44$), importance of shade-tolerant conifers ($r = 0.51$), and boulder cover ($r = 0.60$), while it was negatively correlated with foxtail pine importance ($r = -0.47$). Dimensions two and three were not correlated with measured variables, except for the negative correlations of boulder cover ($r = -0.37$) and H' ($r = -0.35$) with dimension three.

Discussion

Size class distributions of foxtail pine in the Klamath Mountains differ by aspect and elevation. At higher elevations, these distributions are skewed towards larger trees, while at lower elevations the skew is towards smaller trees. This trend also characterizes comparisons among aspects, with southern and western exposures having greater abundances of larger trees than northern and eastern exposures. Substrate type had no effect on size class distributions. These patterns were apparent in the NMS and ANOSIM results, which suggested four groups of transects (Fig. 2). Furthermore, the importance of shade-tolerant conifers, species diversity, and boulder cover differed between elevations. Based on these patterns, our hypothesis is that foxtail

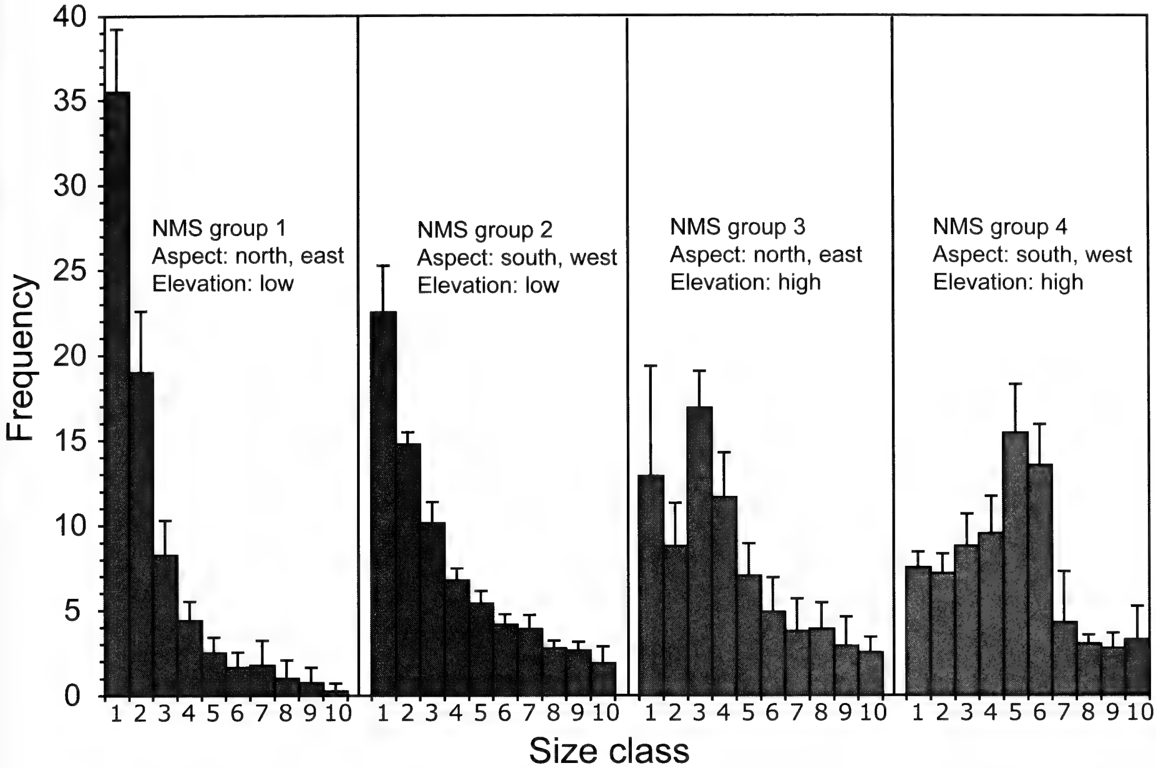

FIG. 3. Average (+ 1 standard deviation) size class distributions of NMS-defined groups.

pine is dispersing into and establishing within downslope stands previously lacking this species as a function of biotic interactions with superior competitors in those stands. We have also related the local distribution of those competitors to two forms of habitat heterogeneity—boulder cover and ultramafic substrates.

The elevation-dependent skew in size class distributions is consistent with the hypothesis that foxtail pine is expanding downslope. The shape of observed size class distributions at low elevations in this study is also consistent with that of growing populations (Harper 1977; Barnes et al. 1998; Silvertown and Charlesworth 2001). The correlation between DBH and tree age bolsters this argument (Eckert and Sawyer 2002). Caution must be used, however, when equating static demographic patterns with trends through time (Clark et al. 1999).

The magnitude of this expansion is localized to downslope areas adjacent to mountaintop foxtail pine stands. The extent of this expansion, therefore, is on the order of a few hectares and has resulted in creating broad ecotones between stands dominated by foxtail pine and downslope stands largely lacking foxtail pine. Furthermore, it appears that this expansion has begun during the past 500 to 1000 yr based on a simple interpretation of the raw demographic data presented in this study (Fig. 3). That interpretation, however, relies on the assumption that previous rounds of expansion into lower elevations would have left traces in the form of snags or downed trees. The wet climate of the Klamath Mountains makes this unlikely, so those dates need to be interpreted with extreme caution.

Several environmental variables were shown to affect the distribution of shade-tolerant conifers (Table 3). Eckert (2006a) showed that these species out-compete foxtail pine based on an analysis of two morphological indices indicative of competition. Therefore, we hypothesize that it is the distribution of shade-tolerant conifers that constrains the ability of foxtail pine to expand downslope. This is consistent with aspect differentially affecting size class distributions of foxtail pine. Southern and western aspects also had decreased importance values of shade-tolerant conifers, as well as, decreased densities and basal areas of shade-tolerant conifers in downslope stands (data from Eckert [2006a]; ANOVA: $F_{3,12}$ = 4.111, P = 0.032). Therefore, we conclude that aspect and boulder cover interact to affect the distribution of shade-tolerant competitors, which in turn constrains, or at least affects, the ability of foxtail pine to expand downslope. In other words, foxtail pine is able to expand downslope better on south and west aspects, because shade-tolerant competitors are not as dominant.

Substrate type affected the distribution of shade-tolerant competitors, with ultramafic substrates having stands with decreased importance values of *Abies concolor*, *A. magnifica* ssp. *shastensis*, and *Tsuga mertensiana*. However, substrate had no effect on the size class distributions of foxtail pine. If the hypothesis discussed above is correct, then this result is enigmatic because foxtail pine should also have strong patterns of downslope expansion on ultramafic substrates. That pattern was not observed, which can be explained by the observation that other members of the genus *Pinus* also out-compete foxtail pine for light (Eckert 2006a). This suggests that constraints on downslope expansion may also be tied to the total tree density of downslope stands (i.e., adjacent downslope vegetation where foxtail pine is not the dominant tree). In all cases, the density and basal area of downslope stands were greater than that observed within foxtail pine stands (Eckert 2006a).

Upslope dispersal of shade-tolerant competitors and downslope dispersal of foxtail pine, which would create broad ecotones on sites with high levels of boulder cover, could also explain our results. This interpretation agrees with the observed decrease of shade-tolerant conifers, which dominate most downslope transects, and boulder cover as elevation increases. If this hypothesis is correct, we would expect to observe similar patterns for co-occurring conifers except in reverse (i.e., lower elevations outside of foxtail pine stands should contain the largest individual trees). These patterns, however, are not found in downslope stands, suggesting that it is foxtail pine that is expanding downslope (data from Eckert [2006a]). Moreover, DNA sequence data for foxtail pine obtained from all sampled stands are consistent with the argument of population growth and expansion from severe population bottlenecks (Eckert 2006b).

Our results, however, are also consistent with other explanations, such as spatially localized resource distributions (e.g., soil nutrients), disturbance regimes, or growth patterns of foxtail pine. For example, the basal areas of stands with western aspects were significantly smaller than those on northern, eastern, and southern aspects. This suggests that growth may differ among aspects as a function of moisture availability. The data, however, do not support similar effects on the local distribution of shade-tolerant conifers, suggesting that our inferences concerning their effects on the ability of foxtail pine to expand downslope may be robust to microclimatic differences between aspects.

Most importantly, we have not addressed the role of climate as affecting our results. Climate is likely to jointly confound the downslope expansion of foxtail pine and the distribution of co-occurring conifers. However, this study has provided the appropriate ecological context for interpreting future climate data. In other words, we have illustrated that there is a strong ecological component to foxtail pine's response to local and regional climate differences and future changes in the Klamath Mountains.

Implications

Size class distributions of foxtail pine in the Klamath Mountains are consistent with the localized expansion of this species into downslope vegetation. Moreover, this expansion is correlated with the distribution of shade-tolerant conifers, which are in turn correlated with habitat heterogeneity (i.e., boulder cover and ultramafic substrates). The implications of such correlations are that the localized expansion by an inferior competitor (e.g., foxtail pine) into habitats dominated by superior competitors (e.g., shade-tolerant conifers) can be facilitated by habitat heterogeneity. Our findings indicate that although historical climate change could be the driving force behind the observed expansions, there exists a strong ecological context to the outcome of downslope expansion by foxtail pine within the Klamath Mountains. Future studies addressing the role of climate in this region, therefore, need to take into account such contexts.

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FLOODPLAIN VEGETATION AND SOILS ALONG THE UPPER SANTA ANA RIVER, SAN BERNARDINO COUNTY, CALIFORNIA

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ABSTRACT

The patterns of vegetation and soils were documented in an approximately 20 km² area of fluvial terraces adjacent to the Santa Ana River in southwestern San Bernardino County, California. Within this area there are three terraces of differing elevations that were last disturbed during major flood events. The oldest terrace surfaces probably were last disturbed during the Agua Mansa flood of 1862, which disturbed or created many current geomorphic features of the Santa Ana River basin. The most recent disturbance of two other terraces was identified based on photographs of flooding events in 1938 and 1969. Principal component analysis identified three assemblages of species whose distribution corresponded to the three terraces that differed in elevation, soil texture, and age since last disturbance by flooding. Canonical correspondence analysis showed that the assemblages identified by PCA were highly correlated with changes in soil texture and organic matter. The most reliable indicator species were *Heterotheca sessiliflora* and *Lepidospartum squamatum* for the first assemblage (associated with the lowest terrace, and corresponding to early successional assemblages identified by other researchers); *Salvia apiana* and *Senecio flaccidus* for the second assemblage (associated with the intermediate terrace); and *Artemisia californica, Opuntia parryi*, and *Stephanomeria pauciflora* for the third assemblage (associated with the highest terrace). *Eriastrum densifolium* subsp. *sanctorum*, the rare Santa Ana River Woolly Star, was associated with the earlier phases of succession. The most important soil factor distinguishing these assemblages was the silt/clay content of the soil.

Key Words: alluvial scrub, *Eriastrum densifolium* subsp. *sanctorum*, floodplain, Santa Ana River, soil texture, succession.

Much of the floodplain vegetation of the Santa Ana River has been extensively modified by channelization, urban encroachment, or water table lowering, and now may be modified further by the recent construction of the Seven Oaks Dam. This 152.4 m high dam is located where the Santa Ana River emerges out of the San Bernardino Mountains on to a large flood plain that is north of the City of Redlands and south of the City of Highland in San Bernardino County (Fig. 1).

Baxter (1977) and Nilsson and Berggren (2000) have presented extensive discussions of the environmental effects of such dams. A major reported effect is that they dramatically reduce the downstream incidence of flooding and reduce the sedimentation and scouring that are often associated with the rejuvenation of early successional habitats. Dams also trap much of the sediment that would normally be transported downstream, resulting in relatively clear water being released below the dam. Clear water tends to pick up a new sediment load from the area downstream, eroding the stream bed, cutting a deeper stream course channel, and further reducing the likelihood of new sediments escaping the channel and rejuvenating the adjacent habitats in subsequent flooding events.

Vegetation associations in a floodplain often reflect differences in flooding frequency and intensity. Early successional plant species tend to establish in the open areas adjacent to the river course that are more frequently flooded. Species on more elevated sites, which are much less frequently flooded, tend to support mid-successional plant communities. Still more elevated terraces, which are only flooded during extreme events, tend to support late-successional or mature associations characteristic of that geographical region (Blom and Voesenek 1996).

In Southern California, many of the remaining unmodified alluvial valleys, outwash fans, and riverine deposits support an open scrub containing taxa from adjacent coastal sage scrub, chaparral, a few species also found in the California deserts, and several local endemics (Ingles 1929). Hanes (1984) described the vegetation occupying most of the floodplain of the upper Santa Ana River as alluvial scrub. This

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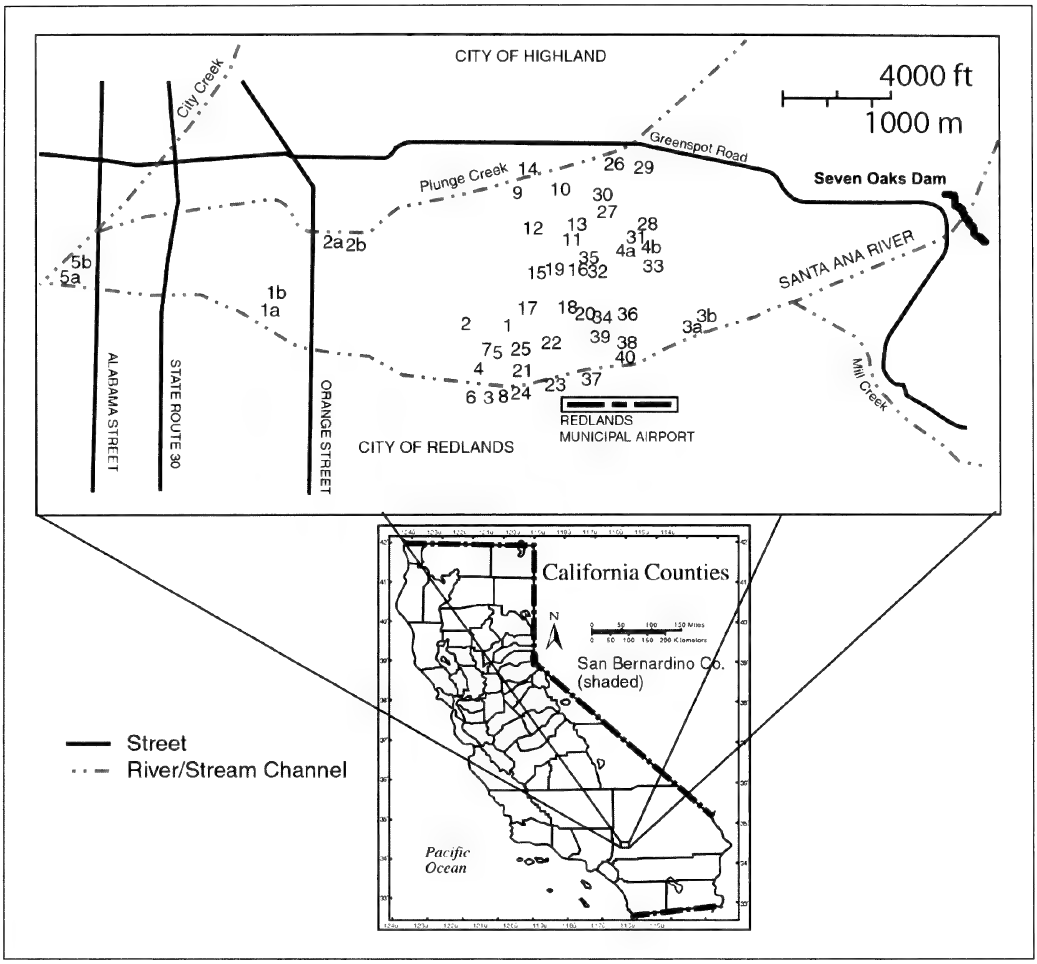

FIG. 1. Locations of the study area and sample sites in floodplain vegetation of the Santa Ana River, San Bernardino County, California. Central map elevation is 425 m. The location of the Seven Oaks Dam is indicated on the far right hand side, just east of where Greenspot Road crosses the Santa Ana River.

vegetation also has been referred to as Riversidean alluvial fan sage scrub (in the California Natural Diversity Data Base/Holland classification [Holland 1986]) and southern alluvial fan scrub (Magney 1992). In *Manual of California Vegetation* (Sawyer and Keeler-Wolf 1995), it is termed the Scalebroom series. In this paper, we refer to this vegetation type as the alluvial scrub community (ASC). It is considered a rare natural community in the State of California, with a Rarefind occurrence ranking of 1.1 (CNDDB 2005).

The alluvial scrub community is distinguished from coastal sage scrub (CSS) by the following qualities: 1) it has a greater variety of evergreen shrubs than CSS; 2) it supports chaparral and desert species (e.g., *Rhamnus crocea* Nutt., Rhamnaceae, *Rhus integrifolia* (Nutt.) Brewer & S. Watson, Anacardiaceae, *R. ovata* S. Watson, Anacardiaceae, *Prunus ilicifolia* (Nutt.) Walp., Rosaceae, *Juniperus californica* Carrière, Cupressaceae, and *Yucca whipplei* Torrey, Liliaceae); 3) *Lepidospartum squamatum* (A. Gray) A. Gray, Asteraceae, (scalebroom) is dominant throughout the ASC and rare in CSS; 4) cover of spring wildflowers is greater than in CSS; and 5) riparian woodland species such as *Platanus racemosa* Nutt., Platanaceae, and *Baccharis salicifolia* (Ruiz Lopez & Pavon) Pers., Asteraceae, occur in alluvial scrub but not CSS.

Early vegetation changes following fluvial surface formation have been described for the ASC of the San Gabriel River floodplain (Smith 1980). Smith identified three seres: an open pioneer stage lasting 30–37 yrs, an intermediate stage, and a mature stage supporting large evergreen shrubs at 40–50 yrs after flooding. She observed that these stages tended to be associated with the frequency of flooding events that scour these surfaces and deposit new sediments.

The recently completed Seven Oaks Flood Control Dam on the main channel of the Santa Ana River will substantially reduce the magni-

tude and frequency of major flood events and, thus, modify the various riparian communities downstream along the river (Burk et al. 1987), including the ASC. The Santa Ana River ASC is also vulnerable because of sand and gravel mine activity occurring within the floodplain. The construction of the Seven Oaks Dam and the mining activities within the floodplain could reduce the acreage available for early successional species and change the species composition of the ASC.

The upper Santa Ana River supports three endangered species, the Santa Ana River Woolly Star (*Eriastrum densifolium* (Benth.) H. Mason subsp. s*anctorum* (Milliken) H. Mason, Polemoniaceae), the Slender-horned Spineflower (*Dodecahema leptoceras* (A. Gray) Rev. & Hardham, Polygonaceae), and the San Bernardino Kangaroo Rat (*Dipodomys merriami* Mearns subsp. *parvus* (Rhoades) Elliot, Heteromyidae), all of which are associated with this spatially and temporally vulnerable alluvial scrub community. Therefore, it is important to understand the changes in this vegetation type that follow flood disturbance and the timing of these successional changes in order to develop conservation practices to both preserve these species and maintain the diversity of this sensitive community.

The current study reconstructs successional changes following major flood events by characterizing vegetation patterns and edaphic changes after the formation of the surfaces of differing ages (terraces) by erosion and/or deposition within the overall floodplain. Specifically, our objective is to interpret the chronosequence of vegetation and edaphic patterns found on extant terraces that originated following the largest recorded flood, the Agua Mansa flood of 1862.

Specifically, we hypothesized that:

1) the major terraces of differing elevations, soils, and age since last disturbance would have unique species assemblages;
2) species assemblages would be similar in composition to those reported for the San Gabriel River floodplain;
3) increasing canopy cover as reflected in surface light measurements would be a factor in species composition differences found among terraces; and
4) edaphic factors would be related to time since last disturbance of the terrace and would also be related to differences in species composition differences among terraces.

Methods and Materials

Study Site. This investigation focuses on an approximately 20 km² area bounded by the City of Redlands on the south, the San Bernardino Mountains on the east, the City of Highlands on the north and the San Bernardino International Airport on the west (Fig. 1). The study site tilts gradually east to west at a 1–2% slope. Geomorphology of the site presents a complex of coalesced alluvial fans originating from the Santa Ana River, Mill Creek, Plunge Creek, and City Creek. The oldest of the geomorphic surfaces are mid– to late–Holocene in age, having been highly modified by overland flow that moves fine sediment, and even gravels and cobbles (Wood and Wells 1996). The alluvial surface is irregularly dissected by channels that have avulsed during major flood events.

Fluvial deposits from these frequently flooded channels are sand and gravel beds that are deposited or reworked during major flood events (Mussetter Engineering, Inc. 1999). The period since the surfaces were significantly reworked by flood events is the time interval for succession. Woodruff (1980) has described the upper Santa Ana River alluvial terrace soils as Soboba stony loamy sand. This Soboba soil series consists of nearly level to moderately sloping soils formed from granitic alluvium on alluvial fans. At our study site, the Soboba series surface is grayish-brown stony loamy sand about 25 cm thick overlying alluvium up to over 100 m in depth. These soils are excessively drained, have low fertility, low water-holding capacity, and very high permeability (Woodruff 1980).

In most years, rainfall events do not result in flows that escape the established river channel and, as a result, do not scour or deposit new alluvium over the existing terraces. Known flood events large enough to shape overbank areas through erosion and deposition occurred in 1862, 1891, 1916, 1927, 1938, and 1969 (Mussetter Engineering, Inc. 1999). The Agua Mansa flood of 1862, with an estimated 320,000 cfs, probably inundated much of the Santa Ana River floodplain, disturbing and modifying all of the terraces within our study area. This flood is characterized as a 100-yr event, that is, one that occurs on average only once in a century (USACE 2000).

The U.S. Army Corps of Engineers (USACE 2000) has simulated these historical flood overflows and concluded that the second largest overflows occurred in the similar magnitude floods of 1891 and 1938 (both with 100,000 cfs). These floods created the somewhat lower terraces that are now considered to be the intermediate-aged terraces. Next in magnitude were the floods of 1916, 1927, and 1969 (two events of 32,460 cfs on 25 Jan. 1969 and a second one of 40,495 cfs on 25 Feb. 1969), which also resulted in overbank flows. Aerial photographs from 1938 and 1969 clearly show that terrace surfaces that we consider to be intermediate- and recent-aged respectively were disturbed by floods in those

two years. Flow rates for the 1938 and 1969 floods were recorded on the U.S.G.S. Stream Gauge #11066460 located near Arlington in the City of Riverside, CA (David Lovell, Department of Public Works, San Bernardino County, Personal Communication).

Sample sites. After an analysis of the surfaces (i.e., terrace surfaces) within the study area, sample sites were chosen based on their being included within the three major terraces of differing ages (see Burk et al. 1987 for a detailed map of these terraces). Four sample site locations within the areas created by the 1969 (sample sites 1 and 5) and 1938 (sample sites 2 and 4) floods (Fig. 1) were assigned by two methods. First, ten sites, designated by both numbers (1, 2, 3, and 5) and letters (a–b), were systematically located after mapping the distribution of *Eriastrum densifolium* subsp. *sanctorum* (eds) (Burk et al. 1987). It appeared that several areas that lacked eds were quite similar in vegetation and substrate to adjacent areas containing eds. Therefore, in order to study factors associated with the distribution of this endangered species, sites designated with an "a" were placed randomly within areas occupied by eds, whereas nearby sites of the same age, designated with a "b", contained apparently comparable vegetation but lacked the presence of eds. These plots provided a sampling of terrace surfaces last disturbed during the 1969 and 1938 floods (what we considered to be the young and intermediate–aged terraces).

Forty additional sample sites (grid sample plots) were selected in a stratified random manner on a grid that extended from the northern boundary to the southern boundary through the central section of the floodplain (Fig. 1, all other numbered sites). These sites were selected to thoroughly sample all terraces within the floodplain, including those formed in 1862. The grid contained eight 70 ha cells, each 30 min of latitude and longitude on a side, located from 34°5′00″ to 34°6′30″N and from 117°10′30″ to 117°11′30″W. Six sites were selected per cell: one site in each of the four quarters of the cell and one additional site in both the north and south halves of each cell. Eight sites were subsequently eliminated when they proved to fall outside the floodplain area. Each sample site was located in the field with a Magellan GPS Nav 1000Pro global positioning system (Magellan Navigation, Inc., San Dimas, CA).

Vegetation sampling. In order to characterize the ASC both qualitatively and quantitatively, plant species cover at each site was measured using the line-intercept method (Barbour et al. 1998). In the *Eriastrum* comparison sites, a 100-m base line was randomly placed. Three randomly positioned 30-m line transects were then placed perpendicular to this base line. In the grid-selected sample set, each of the 40 samples consisted of a randomly oriented 50-m line transect placed at the randomly selected grid point. Orientation was constrained in order to keep the entire transect on a single fluvial surface and to avoid structures and disturbances. Intercept length to the nearest 5 cm was recorded for woody plants (by species), plus herbaceous plants, bryophytes/cryptogamic crust, litter, and dead shrubs. No attempt was made to distinguish individual herbaceous species since the majority of the sampling was carried out during the dry season. Almost all of the herbaceous cover consisted of introduced annual grasses and herbs. Nomenclature follows Hickman (1993) and voucher specimens are filed at the Fay A. MacFadden Herbarium (MACF) at California State University, Fullerton.

Soils. Over the long term, as fluvial terraces age their soil properties slowly tend to differentiate (Jenny 1941). However, recent work on similar fluvial terraces in the Cajon Wash (a system that empties into the Santa Ana River just west and slightly south of our study area), has showed that silt and organic matter rapidly accumulates during the first 40 yrs after flooding even in the soils of these terraces (McFadden and Weldon II 1987). Specifically, they argue that the vast majority of this rapid accumulation is due to the influx of eolian (airborne) dust. This influx not only increases the organics but also increases the water holding capacity of these soils. Such changes could affect the rate of plant succession in such soils and have a significant effect on the persistence of particular early successional species.

Therefore, soil samples were collected to determine the extent of silt and organic matter accumulation at our sample sites, using separate protocols for the eds comparison sites and the grid sample plots. For the eds comparison plots, a soil sample was obtained from a random location along each 30-m line transect used for vegetation sampling for a total of three sub-samples from each comparison site. For the grid sample plots, soil samples were obtained by taking five sub-samples at 10-m intervals along the 50-m transect starting from a randomly selected point. Soil samples were obtained in an identical manner at all sites: A 25-cm metal cylinder (10-cm in diameter) was forced vertically into the soil, then the upper 10-cm of soil was removed from the cylinder, and the remaining soil, from 15–25 cm depth, constituted the sample. All samples from each sample site were thoroughly mixed and a sub-sample was removed for analysis.

Soil samples were analyzed for texture, organic matter, and salinity. Samples were sieved through

1.25- and 2-mm screens to separate larger fractions. Approximately 100 grams of the < 2 mm fraction were analyzed for texture using the Bouyoucos hydrometer method (ASTM Method D433) after removal of organic matter by combustion as outlined by Cox (1985). Organic matter content of the < 2 mm fraction was determined gravimetrically after burning a 100 g oven-dried sample in a muffle furnace at 500°C for 24 hrs. Silt, combined with clay, is reported as "fines" and represents the < 0.05 mm fraction. Values reported as sand are for the 0.05–2 mm fraction and gravel is defined as the 2–13 mm fraction.

Salinity was determined using the conductance of the supernatant from a mixture of 20 g of < 2 mm soil and 100 cc of deionized water equated to standard solutions of NaCl mg/l converted to soil osmotic potential using Van Hoff's law (after Burk et al. 1987). The units used in the analysis are conductance units of millimohs per meter.

Light measurements. Light levels were measured at each sampling site using a LiCor Model 170 light meter fitted with a quantum sensor and served two separate purposes. Ambient light 30 cm above the ground was expressed as percentage of full unobstructed light above the plant canopy and provided a measure of light transmission through that canopy. Reflected light from the soil surface, measured by turning the sensor toward that surface, was also expressed as a percentage of full unobstructed light. It was used as an indirect measure of soil coverage and color. All light measurements were taken on days with less than 25% cloud cover and never when a cloud shaded the site. These measures were also taken between 1000 and 1600 hrs Pacific Standard Time only, in order to avoid low sun angles. The maximum unobstructed light value for each point was taken as the maximum for that point in order to standardize the data for sun angle. In all measurements, care was taken to orient the sensor perpendicular to the soil surface. The readings were recorded at 5 m intervals (n = 10) along the transect from a randomly selected starting point with the sensor 30 cm above the ground at each point. The percentage of full light for ambient and reflected light at each subsample was then calculated. The means of the ten measured light percentages were used to obtain the values for ambient and reflected light levels for each sample site.

Ordination. In order to describe the nature of the relationships between the vegetation and the environmental factors, principal component analysis (PCA) and canonical correspondence analysis (CCA) were performed on all 50 sample sites using protocols in CANOCO for Windows (ter Braak and Smilauer 1998). Thirty-six units were analyzed: 33 woody plants identified to species plus the 3 general plant groups (herbaceous, cryptogams, and dead shrubs). However, woody species occurring in only one sample were subsequently omitted from the analysis leaving 23 active "species" under consideration. Sample sites 6, 15, 31, 32, 33, 42, 46, and 48 were also eliminated from analysis since they proved to contain extreme values in either soil or cover, leaving 42 active samples. In both PCA and CCA, centering was focused on species. In CCA, rare species were downweighted and there was no rescaling or detrending. Of the 11 measured environmental variables, four factors (fines, organics, sand, and gravel) made significant contributions to the analysis based on evaluation of inflation factors (Burk et al. 1987; Ryan 1995). Monte Carlo tests of the first canonical axis and all canonical axes were run with unrestricted permutations. CCA ordination plots are biplots of species and environmental factors. No transformations of variables were employed in the analyses.

RESULTS

Descriptive Statistics – Descriptive statistics for species cover data and for environmental variables are presented in Tables 1 and 2, respectively. Eight non-perennial plant categories (i.e., herbaceous ground cover and substrate categories) were encountered on the transects. Of these, grass, bare ground, and dead shrubs had the highest overall mean cover values (Table 1). Thirty species of perennial vascular plants occurred on the transects, many of which were only encountered occasionally. Only five species had mean cover values above 2%: *Eriogonum fasciculatum* Benth., Polygonaceae, *Juniperus californica, Eriodictyon trichocalyx, Lepidospartum squamatum*, and *Adenostoma fasciculatum* Hook. & Arn., Rosaceae. Percent cover as reflected in light measurements did not vary significantly with terrace age. Ambient light (% of maximum) reflected from the soil surface was quite high overall, indicating an open habitat (Table 2).

Ordination. The CCA eigenvalue for Axis 1 (0.152) is three times greater than the eigenvalues for the other axes (Table 3). The eigenvalues of the PCA are 0.71, 0.068, 0.053, and 0.043 for Axes 1–4 respectively. We present both the PCA and the CCA results because PCA eigenvalues are substantially higher for Axis 1, suggesting that the relationship between environment factors and species can be determined with CCA.

Axes 1 and 2 of the PCA suggested three species groups and four species without definitive association (Fig. 2). *Eriogonum fasciculatum* (erf) and *Opuntia litoralis* (Engelm.) Cockerell, Cactaceae (ol) were at opposite poles of both axes from

TABLE 1. DESCRIPTIVE STATISTICS FOR SPECIES COVER DATA. Species are listed in descending order of mean % cover as recorded from forty-two 50 m transects. Most species were not encountered in all transects, therefore zero values were included in the calculation of the means. All forty-two sample sites are included.

Species	Mean ± Standard Deviation	Minimum–Maximum
Grass	32.0 ± 20.5	0.5–64.3
Bare ground	14.2 ± 13.6	0.3–59.5
Dead shrubs	9.5 ± 6.5	0.2–28.9
Eriogonum fasciculatum	6.2 ± 6.8	0.0–32.5
Bryophytes/cryptogamic crust	5.3 ± 5.5	0.0–27.0
Tall herbs	5.1 ± 3.9	0.0–15.4
Stone	3.3 ± 4.4	0.0–25.2
Juniperus californica	3.0 ± 6.6	0.0–22.7
Eriodictyon trichocalyx	3.0 ± 3.9	0.0–15.9
Lepidospartum squamatum	2.5 ± 4.9	0.0–25.2
Adenostoma fasciculatum	2.2 ± 5.5	0.0–24.7
Gutierrezia californica	1.8 ± 0.5	0.0–11.9
Yucca whipplei	1.7 ± 2.6	0.0–13.3
Low herbs	1.6 ± 1.8	0.0–7.0
Lotus scoparius	1.4 ± 1.9	0.0–7.0
Bebbia juncea	1.1 ± 2.9	0.0–11.8
Prunus ilicifolia	0.8 ± 4.3	0.0–26.4
Opuntia littoralis	0.8 ± 1.3	0.0–4.8
Salvia apiana	0.7 ± 2.3	0.0–11.0
Encelia farinosa	0.6 ± 1.9	0.0–8.0
Artemisia californica	0.5 ± 1.5	0.0–7.1
Mirabilis californica	0.5 ± 1.2	0.0–5.5
Rhus ovata	0.4 ± 1.9	0.0–12.3
Stephanomeria pauciflora var. *pauciflora*	0.3 ± 0.8	0.0–4.3
Ericameria pinifolia	0.3 ± 0.9	0.0–4.4
Opuntia parryi	0.3 ± 0.7	0.0–2.8
Bunchgrass	0.2 ± 0.8	0.0–3.8
Eriastrum densifolium subsp. *sanctorum*	0.2 ± 0.8	0.0–5.1
Phoradendron densum	0.1 ± 0.5	0.0–3.1
Cercocarpus betuloides	0.1 ± 0.7	0.0–4.3
Marah macrocarpus var. *macrocarpus*	0.1 ± 0.5	0.0–3.0
Solanum xanti	0.1 ± 0.4	0.0–2.2
Senecio flaccidus var. *douglasii*	0.1 ± 0.3	0.0–1.8
Cuscuta sp.	0.0 ± 0.3	0.0–1.8
Gnaphalium californicum	0.0 ± 0.2	0.0–1.5
Croton californicus	0.0 ± 0.1	0.0–0.7
Dudleya lanceolata	0.0 ± 0.0	0.0–0.1
Calystegia macrostegia	0.0 ± 0.1	0.0–0.4

TABLE 2. DESCRIPTIVE STATISTICS FOR MEASURED ENVIRONMENTAL VARIABLES. All forty-two sample sites are included.

Variable	Mean ± Standard Deviation	Minimum–Maximum
Litter cover (%)	56.9 ± 26.8	0.0–99.0
Clay particulates (%)	2.4 ± 1.0	0.2–4.3
Silt particulates (%)	7.0 ± 3.5	1.7–15.6
Sand particulates (%) – (sand)	90.5 ± 3.5	82.3–96.2
Fine particulates (clay + silt %) (fines)	9.5 ± 4.1	3.9–17.7
Salinity/conductance (millimohs/m)	0.4 ± 0.3	0.1–1.0
Organic Matter (% dry weight) – (Organics)	0.6 ± 0.6	0.2–4.0
2–13 mm soil particles (% dry weight) (gravel)	10.5 ± 6.9	2.1–33.6
< 2 mm soil particles (% dry weight)	87.7 ± 7.7	65.3–97.6
Ambient light (% of maximum)	81.3 ± 11.2	50.6–99.6
Reflected light (% of maximum)	8.2 ± 3.3	4.2–23.6

TABLE 3. SUMMARY OF CANONICAL CORRESPONDENCE ANALYSIS OF FLOODPLAIN COMMUNITIES OF THE SANTA ANA RIVER NEAR REDLANDS, CALIFORNIA. Input data included 42 samples, 23 species with 490 occurrences and 4 environmental variables. ** Indicates that a particular canonical axis was significantly ($P \leq 0.01$) correlated with environmental factors.

Statistic	Axis 1	Axis 2	Axis 3
Eigenvalue	0.152	0.057	0.035
Species/environment correlations	0.677**	0.5989**	0.579**
Cumulative % variance of species data	9.6	13.2	15.4
Cumulative % variance of species-environment relation	58.1	79.8	93.2

Juniperus californica (jc) and *Lotus scoparius* (Nutt.) Ottley, Fabaceae (los) and thus had quite different affinities and are not included in any of the three groups. (Species are identified with symbols used throughout this paper.)

The CCA correlations between species and environment ranged from 0.462 for Axis 4 to 0.677 for Axis 1. The relationship between species and the four environmental variables was highly significant ($P \leq 0.01$). The cumulative percent of the variance of the species-environment relation indicates that the environmental conditions measured were probably important contributors to species distribution.

The CCA biplots of species scores and environmental factor scores in Fig. 3A showed that Axis 1 was related first ($r = -0.61$) to the amount of fines and secondly to organics ($r = -0.47$). Axis 2 was related ($r = -0.32$) principally to organics. Axis 3 was related to gravel ($r = +0.49$) and sand ($r = -0.51$) (Fig. 3B). Table 4 presents the statistics on the major environmental variables. The relationship between individual species and the environmental axes as determined from t-value biplots showed that multiple species had significant correlations with the environmental axes (Table 5).

When species scores in Fig. 3A were projected to the lines representing fines, three groupings of species were apparent. *Heterotheca sessiliflora* (Nutt.) Shinn., Asteraceae (hf), *Encelia farinosa* Torrey & A. Gray, Asteraceae (ef), and *Lepidospartum squamatum* (ls) were consistent indicators of soils with the least silt and clay content. All of the species that fell on the negative side of Axis 1 were associated with higher silt/clay content and formed a second group that, with the exception of the outlier *Croton californicus* Muell. (Euphorbiaceae [cc]) were the members of PCA Group 3. The third cluster had affinity with soils of intermediate silt/clay content and included all species between *Yucca whipplei* (yw) and *Ericameria pinifolia* (A. Gray) H. M. Hall (Asteraceae [ep]). The third cluster was a mixture of PCA Group 2 and 3 species. Organics correlated with Axes 1 and 2 almost equally and were the only important correlate of Axis 2. Therefore, little interpretable separation occurred on Axis 2. CCA Axis 3 was correlated almost equally with sand and gravel (Fig. 3B). When species centroids were projected perpendicular to the line representing sand, the species from PCA Group 1 formed a group at higher concentrations of sand. PCA group 2 intermingled with PCA Group 1 on Axis 3.

The last two columns in Table 5 show the axis tolerance for each species on Axes 1 and 3 of the CCA ordination. A low value indicates a narrow niche breadth for the principal environmental factor driving each axis and thus identifies indicator species for each PCA group. Axis 2 is not included because of a lack of interpretable separation on that axis.

DISCUSSION

Species cover data document that the upper Santa Ana River alluvial zone is an open habitat supporting a diversity of annual and perennial plant species including, in some, but not all sites, the rare Santa Ana River Woolly Star (eds). Measured environmental variables show that the soils are characterized by a high content of sand or particles > 2 mm in size and that the percent of ambient light reaching the soil surface is quite high in all terraces, again indicating that the habitat is quite open. These features are expected in periodically flood-rejuvenated floodplain habitats.

Regarding succession within alluvial scrub, our findings are consistent with those of Smith (1980) and Hanes et al. (1989) who concluded that there are three seral stages apparent in southern California alluvial scrub vegetation following major disturbance of terraces by flood. Our data, however, suggest much longer periods of dominance for each seral stage and redefine the two later seral stages described by Hanes et al. (1989) and Smith (1980).

In our data, terraces differed in plant assemblages, soil attributes, and time since a major flood disturbance. The dominant plants and edaphic conditions that characterized each of the terraces are as follows. The first asemblage was indicated by the presence of *Lepidospartum squamatum* and/or *Heterotheca sessiliflora*. Terraces that were modified by the 1969 flood supported this assemblage. *Encelia farinosa* was also dependably found on soils characterized by high sand, and low organic and clay content

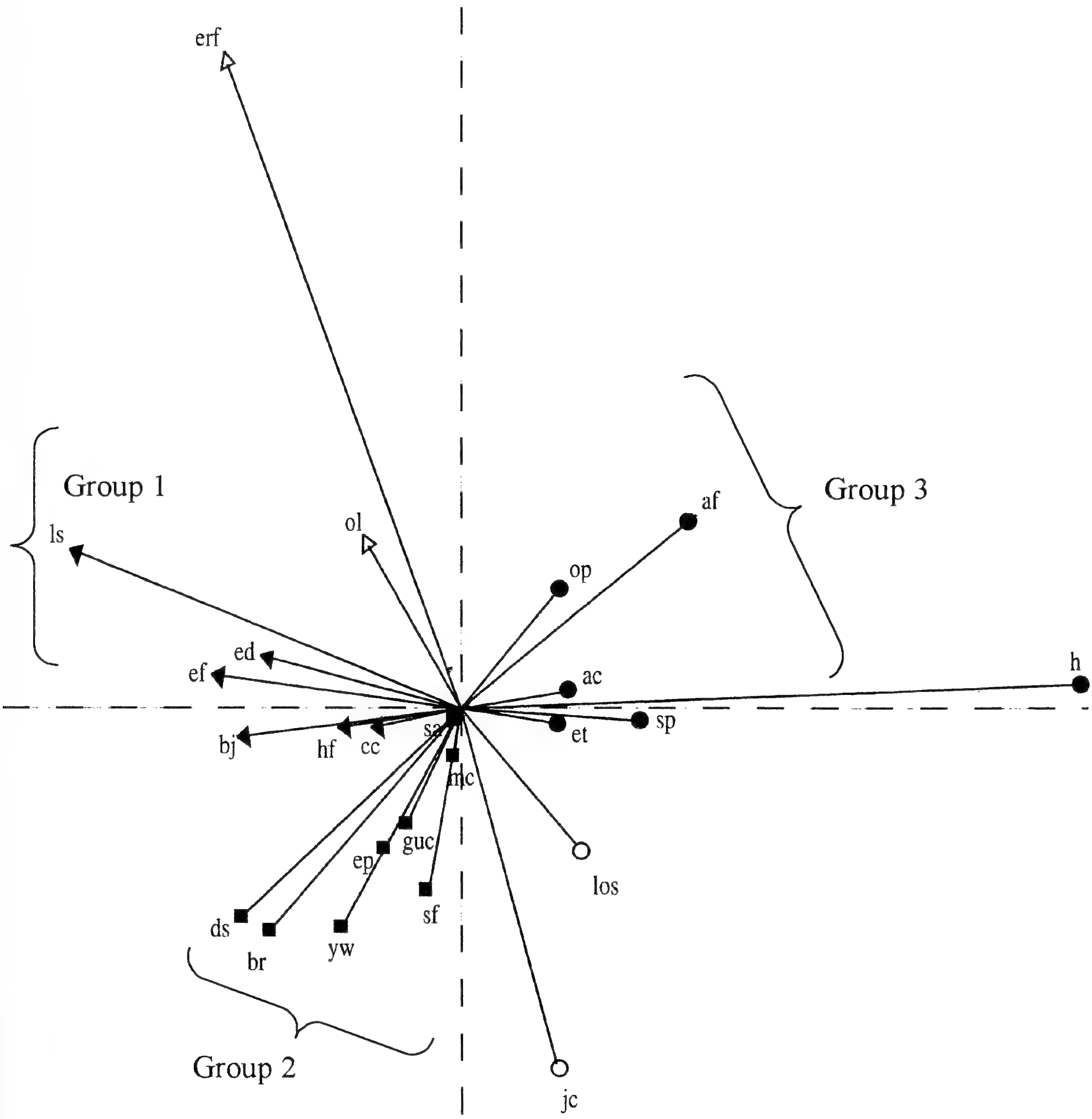

FIG. 2. Principal components analysis axis 1 (horizontal) and axis 2 (vertical) for upper Santa Ana River floodplain species scores. The delimited groups are the PCA groups referred to in the text. Open symbols represent species with no group affinity. Species codes are explained in Table 5. In comparison to Fig. 3, this figure is rotated 180°.

(which were characteristic of the lower elevation terraces disturbed by the 1969 flood), but was not widely distributed. Other plants with centroids in the first assemblage included the endangered *Eriastrum densifolium* subsp. *sanctorum* and the more common *Bebbia juncea* (Benth.) E. Greene (Asteraceae). *Croton californicus* also had its centroid in this group but it was generally distributed and, therefore, was of little value as an indicator.

Hanes et al. (1989) and Smith (1980) refer to this first assemblage as the pioneer community. It is pioneer only in the sense of being first after flood. It contains essentially no ruderal (r-selected) species, probably because the washed sand substrate lacks nutrient and water holding capacity and is, therefore, nutrient limited. *Eriogonum fasciculatum* was not clearly associated with this early seral stage in our data; rather it proved to be an isolated species whose distribution was difficult to interpret. However, Smith (1980) and Hanes et al. (1989) did find that *E. fasciculatum* was an early successional species, unlike the case in our study.

The character of the other two assemblages in our study differed significantly from the intermediate and mature stages described by Hanes et al. (1989) and Smith (1980). *Malosma laurina*

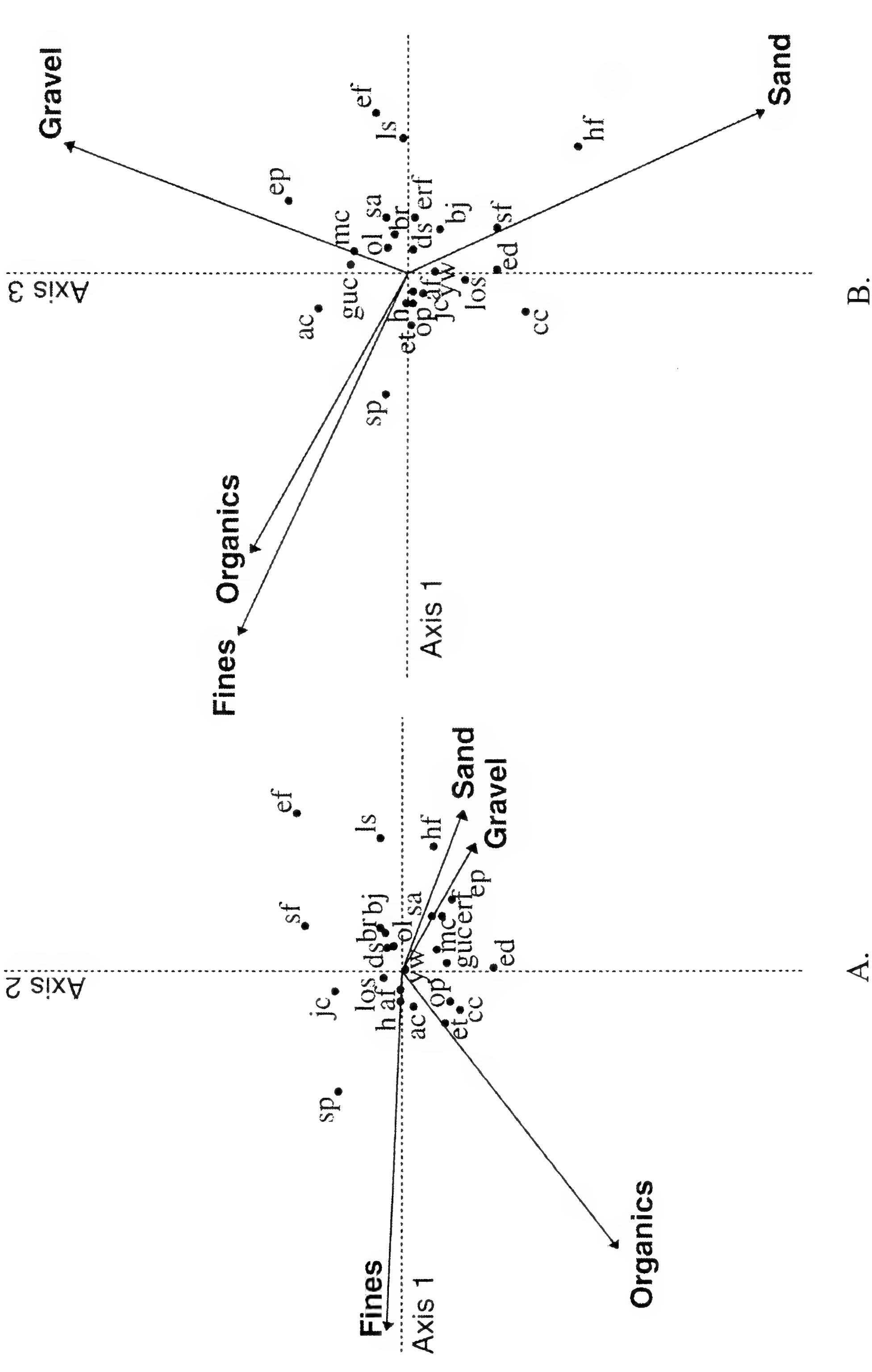

FIG. 3. Ordination diagrams from canonical correspondence analysis showing the distribution of plant species on (A) axes 1 and 2 and (B) axes 1 and 3 relative to 4 environmental gradients in floodplain communities of the upper Santa Ana River, California. Species codes are listed in Table 5.

TABLE 4. SUMMARY STATISTICS FOR SOIL FEATURES INCLUDED IN THE CANONICAL CORRESPONDENCE ANALYSIS OF FLOODPLAIN VEGETATION ALONG THE UPPER SANTA ANA RIVER, CALIFORNIA.

Statistic	Gravel	Sand	Fines	Organics
Mean (%)	9.2	82.0	8.5	0.4
Standard deviation	6.0	10.1	4.7	0.2
Minimum	0.7	61.3	1.4	0.1
Maximum	23.2	98.6	17.7	1.0

(Nutt.) Abrams (Anacardiaceae), *Rhus integrifolia, Ribes aureum* Pursh. (Grossulariaceae), and *Salvia mellifera* E. Greene (Lamiaceae), which Smith (1980) considered indicators of the mature stage, did not occur in our samples and are uncommon in the upper Santa Ana River floodplain. Smith indicated that her mature stands were 47+ years old, which roughly corresponds to the age of stands on terraces last disturbed in 1969 in the current study.

The second assemblage on the upper Santa Ana River alluvial zone supports *Senecio flaccidus* Less. (Asteraceae) and *Salvia apiana* Jepson (Lamiaceae), which had narrow distributions on soil gradients, and were, therefore, good indicator species. Additional shrubs with centroids in the intermediate assemblage were *Ericameria pinifolia* and *Yuccca whipplei.* The presence of cryptogamic crust and dead shrubs was also noted in this phase. Other species found in the second assem-

TABLE 5. LIST OF SPECIES INCLUDED IN THE SAMPLES. Codes and PCA Group are included for those species in the ordinations. A (?) indicates an unclear group affiliation, an (*) indicates a significant ($P \leq 0.05$) correlation between the species and the environmental factor and (ns) indicates non-significance. Axis tolerance is the root mean squared deviation for each species on axes 1 and 3.

Species	Code	PCA Group	Fines	Organics	Sand	Gravel	Axis 1 Tolerance	Axis 3 Tolerance
Adenostoma fasciculatum	af	3	ns	ns	*	ns	0.97	0.92
Artemisia californica	ac	3	ns	ns	*	*	0.76	0.90
Bebbia juncea	bj	1	ns	ns	*	*	0.76	0.86
Croton californicus	cc	1	ns	ns	ns	ns	1.63	0.78
Encelia farinosa	ef	1	*	*	*	*	0.24	0.43
Eriastrum densifolium	ed	1	*	ns	*	*	1.68	0.85
Ericameria pinifolia	ep	2	*	*	*	*	1.24	1.20
Eriodictyon trichocalyx	et	3	*	*	*	*	1.18	0.88
Heterotheca sessiliflora	hf	1	*	ns	*	*	0.04	0.29
Juniperus californica	jc	?	*	ns	*	*	0.81	0.79
Lepidospartum squamatum	ls	1	*	*	*	*	0.86	1.29
Lotus scoparius	los	?	*	ns	ns	ns	0.76	0.60
Mirabilis californica	mc	2	*	ns	*	ns	0.80	0.93
Opuntia litoralis	ol	?	ns	*	*	*	0.88	1.07
Opuntia parryi	op	3	*	ns	*	*	0.74	0.92
Salvia apiana	sa	2	*	*	*	*	0.39	0.66
Senecio flaccidus	sf	2	*	ns	*	*	0.31	0.18
Stephanomeria pauciflora	sp	3	*	*	*	*	0.54	0.97
Yucca whipplei	yw	2	ns	ns	ns	ns	0.88	1.11
Herbaceous plants	h	3	*	*	*	*	0.89	0.98
Dead shrubs	ds	2	*	*	*	*	0.99	0.97
Cryptogams	br	2	*	*	*	*	0.80	1.04

blage were *Gutierrezia californica* (DC.) Torrey & A. Gray (Asteraceae), and *Marah macrocarpus* (E. Greene) E. Greene (Cucurbitaceae). This assemblage was associated with terraces last disturbed by the 1938 flood.

Species with narrow tolerance for soil characteristics in the third assemblage were *Artemisia californica* Less. (ac, Asteraceae), *Opuntia parryi* (op) and *Stephanomeria pauciflora* (Torr.) Nutt. (sp, Asteraceae). Also included in the mature stage were *Eriodictyon trichocalyx* A. A. Heller (Hydrophyllaceae), and *Adenostoma fasciculatum*. *Lotus scoparius* and *Juniperus californica* appeared to be members of both the second and third assemblages.

These second and third assemblages did not correspond to those of Hanes et al. (1989). Hanes (1989) did not differentiate the juniper woodland and chamise associations in terms of environmental variables or stand age, which may be why he assumed that the juniper woodland was associated with a late successional sere. In contrast, in our data, *Adenostoma fasciculatum* was a member of the second assemblage, and *Juniperus californica* was a member of the second and the third assemblages.

Annual herbaceous plants, primarily introduced grasses, were not widespread in this vegetation except on higher terraces. The greater concentrations of clay, silt, and organics on these terraces indicate that sufficient resources exist to support both these resource-demanding grasses and the shrub species of the second and third assemblages that dominate the vegetation of these terraces.

The character of alluvial scrub vegetation of the upper Santa Ana River is highly correlated with soil features that are associated with terrace elevation and likely change gradually with time since the last major flood. In contrast to Smith (1980), we found that changes in alluvial scrub vegetation were correlated with quite small changes in soil texture. In general, with time since last disturbance, there is a gradual increase in the silt/clay and the organic fractions and a coinciding decrease in the relative amount of sand in the soil. These findings are in agreement with those found by Dorronsoro and Alonso (2006) for the fluvial terraces of the Almar River near Salamanca in central western Spain.

The extent to which soil attributes change with time since disturbance is difficult to ascertain. The largest floods on record occurred during the 1860's, including the Agua Mansa flood of 1862. It is generally accepted that the current geomorphology of the upper Santa Ana River was established at that time (Mussetter Engineering, Inc. 1999). Individual *Juniperus californica* trees at one of our sites (2a and b) were established in the late 19th century (personal observation of growth rings indicated they were approximately 100 yrs old). This site fell into our third assemblage, which was associated with the higher elevation terraces, greater clay and silt contents, and the longest interval since disturbance by flooding; this site supported early phase indicators only in isolated microhabitats where rodents or small stream channels have exposed washed sand at the surface. If the vegetation on that terrace was removed in the 1860's, then the early phase was complete and junipers were establishing after 40 yrs.

We have little data that show the impact of large floods, such as the 1891 flood and the 1938 flood, which had recorded flows estimated at half the magnitude of the 1862 flood. It may be that the terrace between the junipers was reworked and flushed in either or both of these floods, thereby extending the early and intermediate stages of succession.

The complex nature of alluvial terraces and the changes that occur with succeeding floods of differing magnitudes make it essentially impossible to map in detail the vegetation of the upper Santa Ana River with regard to successional status. There are many areas where the general vegetation is in the mature phase but small recently eroded channels form fingers of early successional habitats as narrow as 1 or 2 m wide.

The sensitive nature of alluvial scrub species composition to changes in clay, silt, and organic matter suggests that airborne dust from mining operations, construction, or other activities settling in alluvial scrub habitats results in a relatively rapid (within 40 yrs) accumulation of fines and organics decreasing the permeability of the original sand deposits (McFadden and Weldon II 1987) and, as a result, may possibly contribute to the changes in species composition, as was also suggested by McBride and Stone (1976) for sand dune habitats. Because this would shorten the time that this increasingly rare community can persist between floods, this topic merits additional investigation.

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COMPOSITION AND STRUCTURE OF A WEST TEXAS SALT MARSH

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ABSTRACT

This study describes the distribution of species in a 21.6 ha inland salt marsh, consisting of three plant communities. The marsh community is along Leon Creek in the Diamond Y Spring Preserve in Pecos County near Fort Stockton, in western Texas (31°00.54′N, 102°55.49′W). From driest (highest elevation) to wettest (lowest elevation), the sequence is a *Sporobolus airoides* (alkali sacaton, Poaceae) grassland, a *Distichlis spicata* (saltgrass, Poaceae) grassland, and in the drainage a *Schoenoplectus americanus* (bulrush, Cyperaceae) marsh community. The communities were simple, with a total of 15 species found in the marsh. The mean plant cover in the salt marsh was 59%. The *Sporobolus* grassland covered 26% of the marsh and contained six species including *S. airoides* with 52 ± 36% cover and *D. spicata* with 13 ± 21% cover. The four other species were *Helianthus paradoxus* (Pecos or puzzle sunflower, Asteraceae), *Suaeda calceoliformis* (seepweed, Chenopodiaceae), *Limonium limbatum* (sea lavender, Plumbaginaceae), and *Sesuvium verrucosum* (sea purslane, Aizoaceae) (<5% cover each). The *Distichlis* grassland covered 50% of the marsh and contained nine species. *Distichlis spicata* had 50 ± 33% cover followed by *H. paradoxus* at 25 ± 25% cover, *S. calceoliformis* at 10 ± 19% and *S. airoides* at 6 ± 20%. The five other species were *S. texanus* (Texas sporobolus, Poaceae), *Flaveria chlorifolia* (yellow flaveria, Asteraceae), *Juncus mexicanus* (Mexican rush, Juncaceae), *S. americanus* and *L. limbatum* (<2% cover each). In the *Schoenoplectus* community that covered only 2% of the salt marsh, there were 11 species. High cover species included *S. americanus* at 39 ± 33%, *D. spicata* at 22 ± 34%, *H. paradoxus* at 11 ± 26%, and *S. texanus* at 9 ± 14%. Seven other species had cover values of one percent or less including *S. calceoliformis*, *J. mexicanus*, *Samolus cuneatus* (brookweed, Primulaceae), *Spartina pectinata* (prairie cordgrass, Poaceae), *Heliotropium curassavicum* (alkali heliotrope, Boraginaceae), *Agalinis calycina* (Leoncita false foxglove, Scrophulariaceae) and *Eleocharis palustris* (spikerush, Cyperaceae).

Key Words: *Helianthus paradoxus*, inland salt marsh, puzzle sunflower, saltgrass, Texas, wetland.

In the past, saline habitats were reported from many areas of the Chihuahuan Desert Region of western Texas, New Mexico, and northeastern Mexico (Henrickson 1977). Wetland habitats associated with rivers, streams, and springs throughout this part of North America, including western Texas, have almost completely disappeared because of anthropogenic lowering of the water table (Brune 1981; Poole 1992; Poole and Diamond 1993; Horne and Kahn 1997). One of the few remaining wetland systems, an inland salt marsh, is associated with the desert springs found along Leon Creek in the Diamond Y Spring Preserve in Pecos County near Fort Stockton, Texas (Veni 1991; Boghici 1997).

Inland salt marshes are located in continental rather than coastal regions (MacNae 1968; Chapman 1974, 1977; Niering and Warren 1980; Haines and Dunn 1985; Odum 1988). They differ from coastal salt marshes because there are no tidal effects, but they are subject to high variation in soil-salt concentrations and time of desiccation, because of high annual variability of precipitation (Borchert 1971; Ungar 1974). Salt concentrations can range from <1% to >25%, composed variously of Na, K, Mg, or Ca cations and Cl, CO_3 or SO_4 anions (Flowers and Evans 1966; Ungar 1970; Burchill and Kenkel 1991; Venie 1991).

Community composition and structure as well as the various salt gradients of many of the inland salt marshes of other parts of North America have been reported (Billings 1945; Chapman 1974; Henrickson 1977; Flowers and Evans 1966; Ungar et al. 1969; Ungar 1970; Burchill and Kenkel

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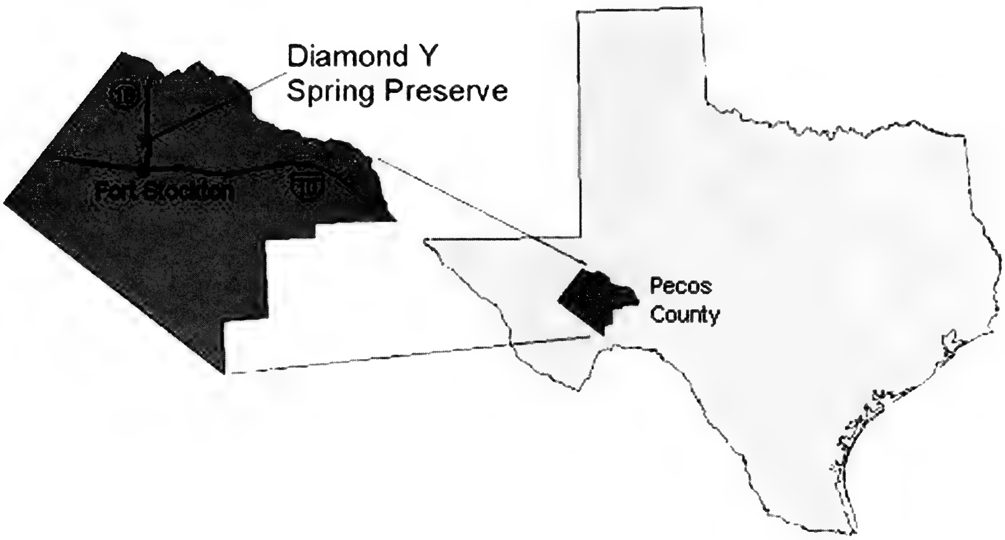


FIG. 1. Location of the Diamond Y Spring Preserve, Pecos County, Texas.

1991). Vegetational zonation, described for marine salt marshes (Chapman 1977; Niering and Warren 1980; Bertness 1991a) is present in various inland salt marshes, with the most salt tolerant species located in the lowest part of the marsh (Chapman 1974; Burchill and Kenkel 1991). This zonation is probably paralleled by one or more environmental gradients (Bertness 1991a; Bertness and Hacker 1994), and may be modified by herbivory and competition (Reinold et al. 1975; Smith and Odum 1981; Bertness 1991a, b; Furbish and Albano 1994). The gradients, communities and species distributions seem to be more complicated in inland salt marshes because of the arid nature of the uplands in many areas, which is not the case in most coastal marshlands (Chapman 1974; Burchill and Kenkel 1991).

The salt marsh found in the Diamond Y Spring Preserve is ecologically important because it is one of few remaining wetland spring communities in western Texas. In addition, it is the location of one of two Texas populations of the federally threatened sunflower, *Helianthus paradoxus* (the Pecos or puzzle sunflower, Asteraceae, Correll and Johnston 1979; McDonald 1999). It is the only recently reported location of a rare Scrophulariaceae, *Agalinis calycina* (Leoncita false foxglove) (Carr 2001; NatureServe Explorer 2006). Additionally, it is the habitat for two federally listed endangered fish, *Cyprinodon bovinus* (Leon Springs Pupfish) and *Gambusia nobilus* (Pecos Gambusia) and three rare snail species (McDonald 1999). However, there is still little information available concerning the plant community types, species composition, and abiotic and biotic gradients present in the wetlands currently existing in western Texas including the Diamond Y Spring Preserve. Population cover, density, and fluctuations of most of the species present in this marsh system have not been established.

The locations of the three major plant communities found in the Diamond Y Springs Preserve have been identified in a previous study (Van Auken and Bush 1998). In addition, some of the soil gradients in this system have been demonstrated including the increase in soil depth, soil water content, and salinity as one proceeds from the upland into the marsh (Grunstra 2002; Grunstra and Van Auken 2007). Soil oxygen content decreases as the soil becomes saturated and seems to be very important for the distribution of some of the species (Bush 2006). Although the minor species present have been identified, their cover, location, and community associations in the marsh have never been determined.

Consequently, the objectives of this study were to identify the minority plant species present and delineate their distributions in the salt marsh along Leon Creek in the Diamond Y Spring Preserve. The three major plant communities were reexamined to help determine population cover and distribution fluctuations from the previous work as well as investigate the associations between the minor plant species and the major plant species and communities located in this salt marsh system.

MATERIALS AND METHODS

Field surveys were conducted in October 1998 in the Diamond Y Spring Preserve of the Nature Conservancy of Texas. The Preserve, consisting of 607 ha of upland and salt marsh communities, is located approximately 13 km north of Fort Stockton, Texas (Pecos County, 31°00.54′N, 102°55.49′W). The site is located on Leon Creek, which flows from Leon Spring and drains into the Pecos River (Fig. 1). The salt marsh has been

grazed and exposed to fires in the past but not in recent years. Soils in the Leon Creek drainage are alluvial, gray-black clays of the Balmorhea Association (Jaco 1980; Rives 1980). Elevation increases slowly away from the drainage, but the soils change dramatically. Orla Association soils are fairly level, somewhat saline, pale-brown loams just upslope from the drainage. Further upland, soils are of the Lozier Association and are light brown to gray, very shallow, gravelly, stony soils on limestone hills (Jaco 1980; Rives 1980).

Species were identified according to descriptions found in Correll and Johnston (1979) and Hatch et al. (1990) with nomenclature updated according to NRCS (2006). The physical location and distribution of all species including species cover or density were estimated in quadrats. The quadrats were located along fourteen permanently marked transects established during a previous vegetation study in the salt marsh (Van Auken and Bush 1998). The transects are located 50 m apart and perpendicular to the drainage from the edge of the *P. glandulosa* savanna on the north to the edge of this same community on the south side of the salt marsh. Transects range in length from approximately 250 to 480 m, depending on the distance across the marsh, and included 50–96 quadrats at 5-m intervals along each transect (n = 1344). Plant cover of all species encountered was visually estimated in 0.1-m quadrat (20 × 50 cm) (Brower and Zar 1977). In addition, all *H. paradoxus* plants in each quadrat were counted in order to obtain the density (Van Auken et al. 2005); this count was done because very large changes in cover of *H. paradoxus* occur from early to late in the growing season because it is a broad-leaved annual.

A grid corresponding to transect sample points was created with AutoCAD© (Autodesk, Inc. San Rafael, CA). Using the Geographic Information System ArcGIS 8.1© and its Geostatistical Analyst extension (ESRI, Redlands, CA), this grid was interpolated into a raster surface plot. Both deterministic and geostatistical interpolation methods were compared using the generated cross-validation error statistics for proper surface interpolation (Johnson et al. 2001). Deterministic methods evaluated were: inverse distance weighted, local polynomial, global polynomial, and radial-based function; geostatistical methods evaluated were: ordinary kriging, simple kriging, and universal kriging. Ordinary kriging was found to give the best predictive surface for the data series and was used for all of the plots presented here. The search radius for the interpolation method was divided into four equal segments with a zero angle of incidence. In each segment, cover or density measurements of five data points were averaged. Contour plots were then prepared for each species using cover or density. Five classes were chosen using smart quantiles (Johnson et al. 2001), which were then approximated in order to encompass all of the generated maps. The five classes were zero, 1–5, 6–15, 16–40, and 41–100.

A generalized map was prepared consisting of the three major communities previously found in the salt marsh (Van Auken and Bush 1998). The three communities were a *Sporobolus airoides* grassland, a *Distichlis spicata* grassland, and a *Schoenoplectus americanus* bulrush marsh. Community limits for the *S. airoides* grassland and the *D. spicata* grassland were established by extrapolation to points on the map where their cover was 25%. Community limits for the *S. americanus* bulrush community were set at 20% cover. These cover values were selected to minimize mapped overlap between communities and areas that could not be classified. Total area of this map and the individual species maps is 21.6 ha.

RESULTS

The apparent exclusiveness of the main perennial species found in the previous study in this west Texas salt marsh was also evident in the current study. For example, along a representative transect, Fig. 2 shows the cover and distribution of two of the most abundant species, *Sporobolus airoides* (alkali sacaton, Poaceae) and *D. spicata* (saltgrass, Poaceae) which were almost mutually exclusive. *Sporobolus airoides* was mainly along the first part of this transect (northwest corner of the study area). It was not present in the center of the transect and then it occurred again (but less consistently) along the last part of the transect (south side of the marsh, Fig. 2). In both parts of this transect, it was found along the edge of the salt marsh, in areas with higher elevation (O. W. Van Auken, personal observation). *Distichlis spicata*, for the most part, had low cover in the first 175 m of this transect (north, Fig. 2), then increased to 30–100% in the next 200 m of this transect and was more sporadic in the last part of the transect (south).

The distributions of the three major communities at the Diamond Y Spring Preserve salt marsh are presented in Fig. 3. The *S. airoides* community was found in the parts of the salt marsh that were slightly higher in elevation (O. W. Van Auken, personal observation) and occupied 5.5 ha (26% of the marsh area) (Fig. 3). These areas were mainly in the northwest part of salt marsh and along the southern edge of the marsh. In the lowest part of the salt marsh along the drainage of Leon Creek, in soils that are saturated for at least part of the year, we found the *S. americanus* community, which occupied 0.4 ha (2% of the marsh area) and

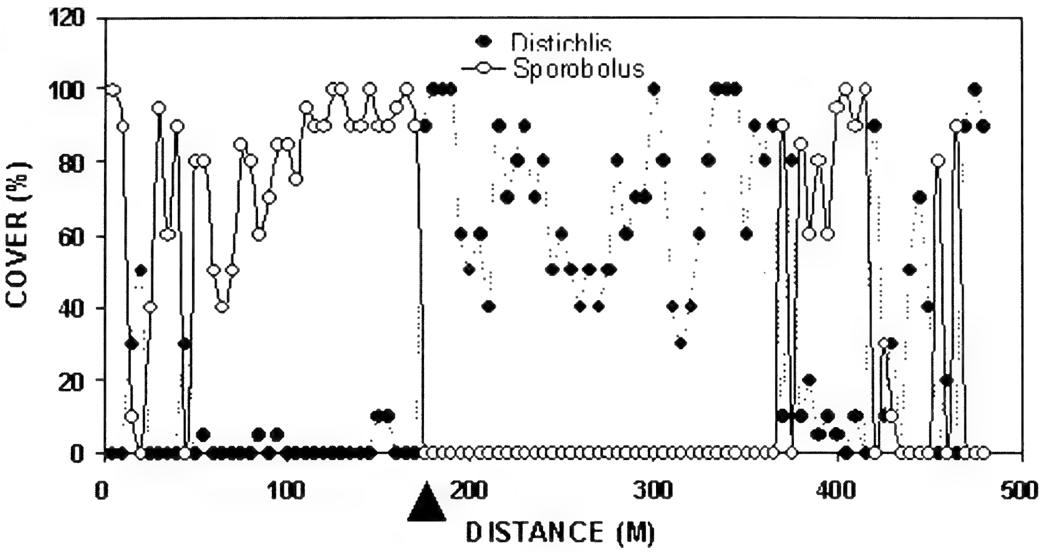


FIG. 2. *Sporobolus airoides* and *Distichlis spicata* cover along a representative transect. This transect extends from the *Prosopis glandulosa* upland vegetation north of the salt marsh (zero) to the creek edge (drainage, lowest part of the marsh), and then to the *P. glandulosa* upland vegetation to the south (500). Each quadrat was 5 m apart. The black triangle below the *x* axis indicates the location of Leon Creek.

was somewhat disconnected (Fig. 3). Between these two communities at intermediate elevations and apparently intermediate levels of soil water saturation is the *Distichlis* community, with the perennial *D. spicata* as the dominant species. This community was extensive in the salt marsh occupying 10.8 ha (50% of the marsh area) (Fig. 3). Overlap between the *Distichlis* and the *Sporobolus* grassland community was 1.4 ha or 6.5% of the total area studied (Fig. 3). Overlap between the *Distichlis* and the *Schoenoplectus* community was 1.0 ha or 4.5% of the area studied. Areas that could not be classified or placed in one of the three community types amounted to 2.4 ha or 11.1% of the total marsh area.

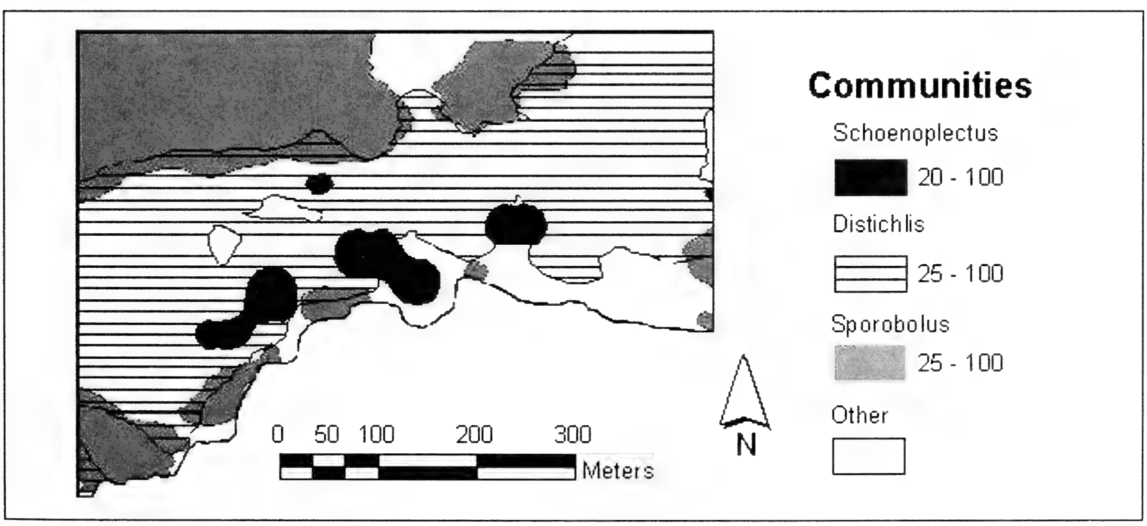


FIG. 3. Distribution of the three plant communities identified along the Leon Creek drainage in the Diamond Y Spring Preserve near Fort Stockton, Texas. The communities are: *Schoenoplectus* = *Schoenoplectus americanus* cover 20–100%, in the wettest part of the marsh; *Distichlis* = *Distichlis spicata* cover 25–100%; and, *Sporobolus* = *Sporobolus airoides* 25–100%, in the highest, driest part of the salt marsh. The dashed line is the Leon Creek drainage. The straight line running north-south in each figure is a dirt road that crosses the salt marsh.

TABLE 1. COVER (%) ± ONE STANDARD DEVIATION FOR EACH SPECIES FOUND IN 0.1-m QUADRATS (N = 1344) IN THE SALT MARSH OF THE DIAMOND Y SPRING PRESERVE NEAR FORT STOCKTON, TEXAS. In addition, the mean cover ± one standard deviation of each species found in each of the three communities identified in the salt marsh is presented. Density (plants m^{-2}) is also presented for *H. paradoxus*. A zero in a column indicates that species was not found in that community. *<1% cover **Density, plants/m^2

	Community Types			
Species	Marsh total	*Sporobolus*	*Distichlis*	*Schoenoplectus*
Distichlis spicata (Poaceae)	24 ± 32	13 ± 21	50 ± 33	22 ± 34
Sporobolus airoides (Poaceae)	16 ± 31	52 ± 36	6 ± 20	0
Suaeda calceoliformis (Chenopodiaceae)	5 ± 14	2 ± 8	10 ± 19	1 ± 3
Schoenoplectus americanus (Cyperaceae)	2 ± 11	0	3 ± 12	39 ± 33
Limonium limbatum (Plumbaginaceae)	1 ± 3	2 ± 5	1 ± 3	0
Sporobolus texanus (Poaceae)	1 ± 6	0	2 ± 10	9 ± 14
Flaveria chlorifolia (Asteraceae)	1 ± 7	0	—*	0
Juncus mexicanus (Juncaceae)	—*	0	—*	—*
Spartina pectinata (Poaceae)	—*	0	0	—*
Samolus cuneatus (Primulaceae)	—*	0	0	—*
Sesuvium verrucosum (Aizoaceae)	—*	—*	0	0
Heliotropium curassavicum (Boraginaceae)	—*	0	0	—*
Agalinis calycina (Scrophulariaceae)	—*	0	0	—*
Eleocharis palustris (Cyperaceae)	—*	0	0	—*
Helianthus paradoxus (Asteraceae)	9 ± 26	4 ± 22	25 ± 25	11 ± 26
Helianthus paradoxus (Asteraceae)	25 ± 71**	2 ± 17**	44 ± 88**	8 ± 22**
Total cover	59	71	97	82

There were 15 species of herbaceous plants in the salt marsh at the Diamond Y Spring Preserve but no woody species (Table 1). *Distichlis spicata* had the greatest mean cover averaged over the whole area of the salt marsh sampled at 24 ± 32% (±SD), followed by *S. airoides* at 16 ± 31% cover (Table 1). *Helianthus paradoxus* cover was 9 ± 26% with a density of 25 ± 71 plants m^{-2} over the salt marsh. Twelve other species had cover values <10%. In the *Sporobolus* community, *S. airoides* cover was 52 ± 36%. Five other species were found in the *Sporobolus* community (Table 1). In the *Distichlis* community, *D. spicata* cover was 50 ± 33% followed by *H. paradoxus* at 25 ± 25% cover and *Suaeda calceoliformis* (seepweed, Chenopodiaceae) at 10 ± 19% cover. Six other species were found in this community with lower cover values (Table 1). The highest mean cover and density of *H. paradoxus* was in the *Distichlis* community at 25 ± 25% and 44 ± 88 plants m^{-2} respectively. In the *Schoenoplectus* community, *Schoenoplectus americanus* (bulrush, Cyperaceae) cover was 39 ± 33%. *Distichlis spicata* and *Sporobolus texanus* (Texas sporobolus, Poaceae), two morphologically similar grasses, had cover values of 22 ± 34% and 9 ± 14% respectively in this community. Eight other species were in this community, for a total of 11 species, making it the community richest in number of species. Variance in cover was high for all species. Standard deviations were approximately half to eight times the mean cover for all species (Table 1).

Spatial patterns of the five species with overall cover values of 1–9% are displayed in Fig. 4. *Limonium limbatum* (sea lavender, Plumbaginaceae) was primarily at slightly higher elevation and associated with the *Sporobolus* community. It was sporadic in the *Distichlis* community, usually in the upper part of this community and decreasing in cover toward the drainage (Fig 4a). This distribution is essentially in the northwestern and southwestern edges of the marsh, somewhat elevated from the drainage and close to the *P. glandulosa* upland community (upland community not shown). *Limonium limbatum* was found on approximately 5.8 ha (26.9%) of the marsh surface with the majority (5.3 ha) having cover values of 1–5% and only 0.5 ha with slightly higher cover values of 6–15% (Table 2).

Suaeda calceoliformis was fairly widespread in the marsh found on approximately 15 ha (69.4%) (Table 2), with most quadrats having cover values in the range of 1–40%. The largest portion of this area (6.3 ha) was at cover values of 1–5%. Higher cover values (6–15%, 16–40%) were found on 4.9 ha and 3.7 ha respectively. *Suaeda calceoliformis* had cover values >40% but only in small areas (0.1 ha) (Table 2). However, *S. calceoliformis* was also encountered in parts of the higher elevation grasslands, where *S. airoides* cover was high (Fig. 4b). *Suaeda* had 1–40% cover in approximately half of the area of the salt marsh sampled with greater cover in wetter parts of the *Distichlis* community.

Sporobolus texanus was only present along the drainage and was associated with standing water in the *Schoenoplectus* community in the wettest part of the marsh. It was never detected with *S.*

airoides in the higher elevation, drier grasslands of the salt marsh (Fig. 4c). *Sporobolus texanus* covered approximately 3 ha (13.9%) of the marsh (Table 2). This area was split between the two lower cover classes. *Sporobolus texanus* did have high cover values, but in small areas (Table 2).

Flaveria chlorifolia (yellow flaveria, Asteraceae), was not usually associated with *S. airoides*, in the drier grasslands of the salt marsh (Fig. 4d). It was only in the wettest part of the salt marsh, which had wet soil year-round (O. W. Van Auken personal observation). It was usually associated with *S. texana* or *S. americanus*, but sometimes it occurred with *D. spicata* and *H. paradoxus*. It was only in the southeastern corner of the salt marsh and covered an area of 2.5 ha (11.6%) (Table 2). *Flaveria chlorifolia* was fairly equally spread over the three first cover classes. *Flaveria chlorifolia* had covers values >40% although this was in <0.1 ha of the marsh (Table 2).

Helianthus paradoxus was detected with densities ≥ 6 plants m^{-2} on more than 20% of the salt marsh sampled, mostly in the *Distichlis* community (Fig. 4e). It was usually not in the *Sporobolus community* or in the *Schoenoplectus* community (which is the wettest part of the salt marsh); thus, *H. paradoxus* was not distributed uniformly across the salt marsh. There were large areas in the *Distichlis* community with few or no *H. paradoxus* and other parts of this community that had high densities. Actually, 36.6% of the quadrats from the *Distichlis* community had some *H. paradoxus* plants and covered approximately 13 ha (60.2%) (Table 2). The majority (7.9 ha) of this area had 1–5 plants m^{-2}. Four and a half hectares had 6–15 plants m^{-2} and 0.6 ha had 16–40 plants m^{-2}. There were no areas with *H. paradoxus* densities >40 plants m^{-2} (Table 2).

Discussion

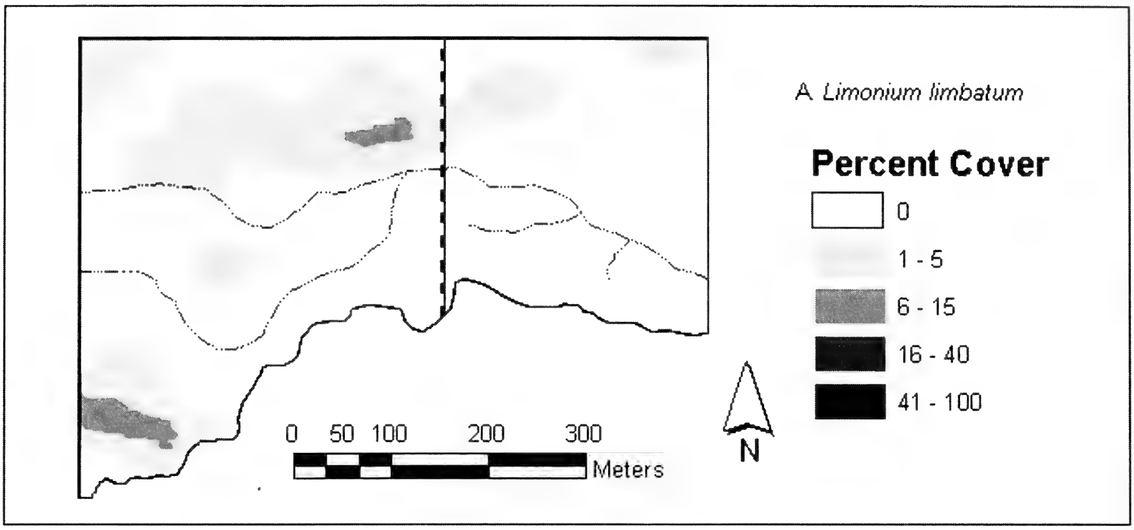
For the most part, community composition, and abiotic and biotic gradients in the inland salt marshes of western Texas and northern Mexico have been largely ignored. Zonation does appear in the Diamond Y Spring Preserve salt marsh as one descends from the slightly higher elevation around the edge of the salt marsh into the center (Fig. 3). The low-density species present in the Diamond Y Spring Preserve salt marsh are found mainly in one community associated with one of the dominant species. However, overall there are very few species present in this salt marsh system.

The reason for the low number of species reported from these salt marsh communities is unknown. Some species that are present in the Diamond Y Spring Preserve could have been missed in the past because of low cover, low density, cryptic nature, seasonality or a clumped population distribution. A low number of species has been reported previously for saline habitats in western Texas and northern Mexico (Hendrickson 1977; Pinkava 1977). The relatively high levels of Na_2SO_4 in the soil of the Diamond Y Spring Preserve (10 to 40 ppt) and the shallow water table (Grunstra 2002) may play a role. These two factors coupled to high cover of *S. airoides* and high total biomass could prevent entry of other species into the *Sporobolus* community. The *Distichlis* community also has few species, but almost twice as many as the *Sporobolus* community. The cover of the *Distichlis* community may be higher than the *Sporobolus* community (Table 2), but the biomass appears to be lower (O. W. Van Auken, personal observation). *Distichlis spicata* is not a perennial bunchgrass, but a perennial sod forming C_4 grass, and it is lower in stature. In addition, more biomass may be removed from this community by large ungulates, but this is undocumented.

Most of the species reported from the salt marsh are not found in the upland *Larrea tridentata* or *Prosopis glandulosa* communities. These upland areas have low levels of salt, but are also probably too dry most of the year for the growth of the salt marsh species. In the lowest part of the salt marsh, the concentration of organic material in the soil, low soil oxygen, or possibly the redox potential of the soil does not seem suitable for growth of some salt marsh species (Bush 2006) or upland species as has been reported for other salt marsh communities (Webb and Mendelssohn 1996).

The largest number of species (eleven) was found in the *Schoenoplectus* community. This community was only present in the drainage or around the springs, in the wettest part of the salt marsh (Fig. 3). The most common species associated with *S. americanus* were *D. spicata* and *S. texanus*. They were usually encountered around the edge of the *Scheonoplectus* community. *Flaveria chlorifolia* had high cover in some of the wettest areas of the salt marsh and it was associated with *S. americanus*, *D. spicata* and *S. texansus*. All of the other species found in this community seemed to occur in ungulate created disturbances around a spring or seep in the wettest part of the marsh. These species have been reported from saline habitats in other parts of western Texas and northern Mexico but not from other non-saline habitats (Henrickson 1977; Pinkava 1977).

The distributions of the primary perennial grass species were not seen to vary in location from the previous study to the current study. On the other hand the distribution of *Helianthus paradoxus* and some of the other minor species shifted greatly in locations. This could be due to



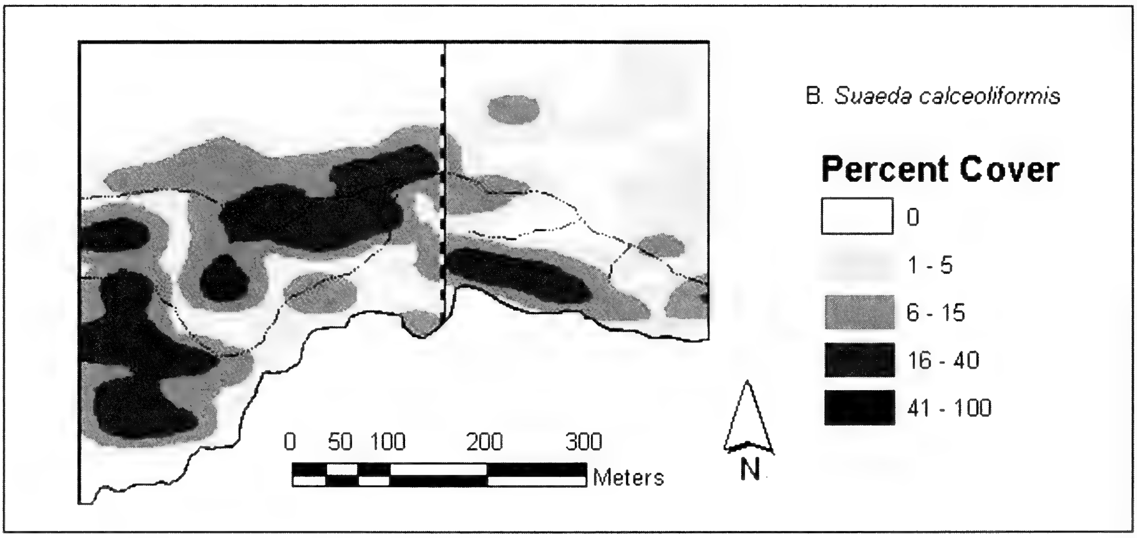


FIG. 4. Distribution of five species in the salt marsh along the Leon Creek drainage in the Diamond Y Spring Preserve near Fort Stockton, Texas. The figure includes: (A) *Limonium limbatum* (sea lavender) percent cover, (B) *Suaeda calceoliformis* (seepweed) percent cover, (C) *Sporobolus texanus* (Texas sporobolus) percent cover, (D) *Flaveria chlorifolia* (yellow flaveria) percent cover, and (E) *Helianthus paradoxus* (Pecos or puzzle sunflower) density. The dashed line is the Leon Creek drainage. The straight line running north-south in each figure is a dirt road that crosses the salt marsh.

a variety of reasons. As annuals, these species could establish in ephemeral gaps produced by grazing, fire, or other disturbance (Bush and Van Auken 1997). Also, temporal and spatial variations in the water level, soil pH, and soil salinity could account for the movement of their distributions (Bush and Van Auken 2004). The specific levels of these abiotic factors during the germination and growth periods of these annuals may influence their individual competitive ability and survivability in the three primary perennial communities (Van Auken and Bush 2006).

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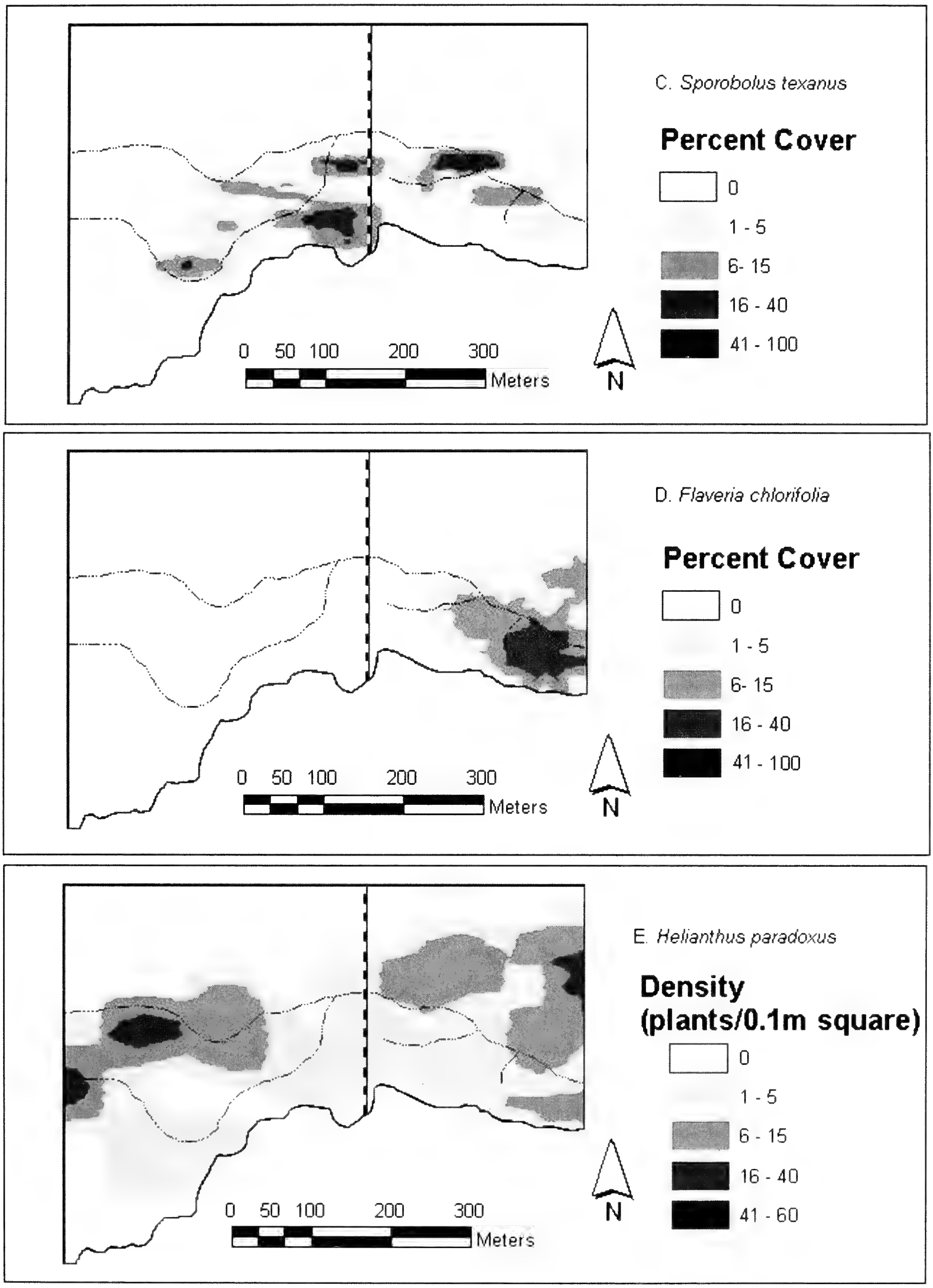

FIG. 4. Continued.

TABLE 2. TOTAL AREA (HA) FOR EACH OF THE FIVE SPECIES WITH OVERALL COVER VALUES OF 1–9% IN THE SALT MARSH OF THE DIAMOND Y SPRING PRESERVE NEAR FORT STOCKTON, TEXAS. Area (ha) is displayed for each of the classes shown in Figure 4. In parenthesis is the percentage of the total marsh area. An * in a column indicates an area <0.1 ha. A zero in a column indicates that species was not found in that class.

Species	Total	Class			
		1–5	6–15	16–40	41–100
Limonium limbatum	5.8 (26.9)	5.3 (24.5)	0.5 (2.4)	0	0
Suaeda calceoliformis	15 (69.4)	6.3 (29.2)	4.9 (22.7)	3.7 (17.1)	0.1 (0.4)
Sporobolus texanus	3 (13.9)	1.4 (6.5)	1.3 (6.0)	0.3 (1.4)	—*
Flaveria chlorifolia	2.5 (11.6)	0.9 (4.2)	1.1 (5.1)	0.5 (2.3)	—*
Helianthus paradoxus	13 (60.2)	7.9 (36.6)	4.5 (20.8)	0.6 (2.8)	0

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TAXONOMIC REVISIONS IN THE GENUS *ARCTOSTAPHYLOS* (ERICACEAE)

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ABSTRACT

Changes are made in the nomenclature of species and subspecies in the genus *Arctostaphylos* (Ericaceae). In this study, the focus is on species found in the coast ranges of California. Changes are made in *A. nortensis* from the area around the Oregon border with California, in the *A. nevadensis* complex in the North Coast Ranges, in the *A. nummularia* complex of the north to central coast, in the *A. tomentosa* complex of the central coast to the Channel Islands, and in the *A. hookeri* and *A. pilosula* complex of the central coast. Also discussed are other changes presented elsewhere that will affect the *Arctostaphylos* treatment in the next edition of the Jepson Manual.

Key Words: *Arctostaphylos*, California, Ericaceae, new combinations.

The genus *Arctostaphylos* represents a quintessentially Californian complex of species that have radiated into a large number of soil types, climates, and plant communities. Philip V. Wells conducted the last major revisions of this genus (1968, 1987, 1988a, 1992, 1993, 2000). Wells developed a vision for the genus that included his typological view of taxa that idealized certain characteristics and overlooked important intra- and inter-population variation such as many bract or nascent inflorescence traits (Wells 1993, 2000). He proposed that a leafy-bracted, resprouting tetraploid complex was the core ancestral group (Wells 1987). For the last several decades we have also taken a systematic interest in this genus (most recently, Keeley and Massihi 1994; Keeley et al. 1997a, b; Markos et al. 1999; Vasey and Parker 1999; Hileman et al. 2001; Parker and Vasey 2004; Boykin et al. 2005; Keeley et al. 2007). These studies have led to a somewhat different view of *Arctostaphylos*, and based on our experience with the group, we propose a number of changes to the current treatment (Wells 1993, 2000) and provide our rationale for these changes.

ARCTOSTAPHYLOS NORTENSIS

After examining specimens in herbaria, plus our own collections from the type locality, we were somewhat confused about the status of widespread populations of an *Arctostaphylos* taxon similar to *A. nortensis* (Wells) Wells but not quite matching the description. These populations were considered as either *A. nortensis* or hybrids referred to by Gottlieb (1968). Our specimens had the general pubescence and inflorescence characters we expected, but also contained glandular hairs. Following pressing and drying, these glandular hairs were somewhat cryptic in some of our collections. While not mentioned in the original description (Wells 1988b), later in his treatments of the genus Wells (1993, 2000) insists that this species has no glandular hairs on any organ. This led us to review the type specimen (*P. V. Wells and W. Knight 8186*, CAS). Here we found numerous glandular hairs, generally longer than most of the pubescence, somewhat different from those on our specimens, which were often shorter than the longest hairs. Nonetheless, we were impressed that the type contained the glandulosity we were seeing in the field. Consequently, we amend the description of *A. nortensis* to include presence of glandular hairs on the branchlets, and often on the petioles and edges of younger leaves. With this amendment, the "rare" status of *A. nortensis* needs to be re-evaluated because of the extensive stands of this taxon present in northern Del Norte County, California, and southern Oregon as well. At the same time, the difference in the type of glandularity among the type specimen, our collections, and Wells' descriptions (Wells 1993, 2000) suggests more research is required for a clearer understanding of this taxon. For example, cuttings from shrubs of the same area

as the type now growing in the Regional Parks Botanical Garden are non-glandular (Stephen Edwards, personal communication). Here we modify Wells' description to match his type specimen.

Arctostaphylos nortensis (P. V. Wells) P. V. Wells, emend. V. T. Parker, M. C. Vasey, J. E. Keeley, description to include usually with glandular hairs.—*Arctostaphylos columbiana* Piper subsp. *nortensis* P. V. Wells, Four Seasons 8(1): 50, 1988. *Arctostaphylos nortensis* (P. V. Wells) P. V. Wells, Four Seasons 9(2): 56. 1992. Type: USA, California, Del Norte Co., Gasquet Toll Road, near Gasquet on serpentinite, *Wells and Knight 8186* (isotype CAS).

Arctostaphylos nummularia Complex

As part of a molecular phylogeny of *Arctostaphylos* (Boykin et al. 2005; Wahlert 2005), *A. nummularia* A. Gray breaks into two groups, one from Mendocino County and northern Sonoma County and one from Marin County and Santa Cruz County. The southern populations, originally named *A. sensitiva* Jeps. (Jepson 1922), were transferred to a variety of *A. nummularia* by McMinn (1939). Further complicating this was Wells' (1989) separation of related populations in the north as *A. mendocinoensis* Wells. What has struck us about published descriptions of these plants is the failure to recognize a significant morphological distinction between the northern and southern populations, specifically a strikingly different bark characteristic. The Mendocino and northern Sonoma County populations have persistent bark, which on small plants retains a slightly red color, but as the plants age, the bark becomes grey and rough or shaggy. The plants in Marin and Santa Cruz counties retain the red, smooth bark throughout their lifespan, as is the case with the majority of *Arctostaphylos* species. McMinn (1939) noted that his conception of *A. nummularia* (which included *A. sensitiva* as a variety) included plants with exfoliating grey-brown or smooth reddish bark. Somehow, knowledge of this variation was lost in later treatments.

Morphologically, a gradual cline exists in characteristics between what Wells (1989) has named *A. mendocinoensis* and other collections of *A. nummularia* in Mendocino County, while southern populations from Marin and Santa Cruz Counties generally differ in characteristics from the Mendocino and Sonoma populations, such as the number of inflorescence branches. Both McMinn (1939) and Wells (1968 in Table 1) noted that the southern populations were generally more robust and less variable than those in the north. *Arctostaphylos mendocinoensis* is a diminutive, relatively prostrate shrub in harsh podsol soils in the pygmy forest which grades imperceptibly into upright shrubs (*A. nummularia*) in adjacent forest and maritime chaparral. As a consequence of the cline between *A. nummularia* and *A. mendocinoensis*, we propose submerging *A. mendocinoensis* as a subspecies of *A. nummularia*. *Arctostaphylos sensitiva* is an important member of maritime chaparral in southern Marin and the central to southern Santa Cruz Mountains, and because of the morphological and molecular disjunction between the northern and southern populations, we propose resurrecting *A. sensitiva* as a species inhabiting the southern region.

Arctostaphylos nummularia A. Gray subsp. **mendocinoensis** (P. V. Wells) V. T. Parker, M. C. Vasey, J. E. Keeley comb. nov.—*Arctostaphylos mendocinoensis* P. V. Wells, Four Seasons 8(3): 30. 1989. Type, USA, California, Mendocino Co., *P. V. Wells, I. Knight, W. Knight 11189* (holotype CAS).

The Arctostaphylos hookeri Complex

Taxonomic confusion has occurred among various clusters of species of *Arctostaphylos* that exhibit simple, elliptic, green leaves. Characters that separate them, such as fruit or nascent inflorescences, were not emphasized early in the taxonomy of *Arctostaphylos*. Wells (1968, 1993, 2000) took 5 of these simple green-leaved taxa and submerged them as subspecies of *A. hookeri* G. Don. *Arctostaphylos hookeri* was one of the earliest named manzanitas (by George Don in 1834), a distinctive endemic of stabilized dunes and upland sandstone habitats in the Monterey area, an area collected by early explorers in the 1800's. The next taxon named from Wells' *A. hookeri* complex was *A. montana* Eastw. (Eastwood 1897), a Marin County serpentine endemic. McMinn (1939) considered this to be a northern population of *A. pungens* and submerged it into *A. pungens*. He mentioned that, without inflorescences, some of the smaller specimens of *A. montana* are difficult to separate from the more erect forms of *A. hookeri* (McMinn 1939). Munz (1958) resurrected *A. montana* as a variety of *A. pungens*. Eastwood (1905) also named *A. franciscana* Eastw., an endemic shrub formerly abundant in serpentine areas in San Francisco. This species suffered a relatively similar fate as did Eastwood's *A. montana* Eastw. because McMinn (1939) submerged it into *A. hookeri*, and later Munz (1958) resurrected it as a subspecies of *A. hookeri*. *Arctostaphylos hearstiorum* Hoover & Roof was first described by Hoover and Roof (1966) and is known only from coastal grasslands of the Hearst Ranch near San Simeon. Finally, a remaining individual of a formerly more

extensive population from serpentine areas of San Francisco found by Peter Raven was named *A. hookeri* subsp. *ravenii* (Wells) by Wells (1968). The range of natural variability of this taxon is unknown.

In one of his first revisions of the genus, Wells (1968) lumped the three serpentine endemic taxa from the northern San Francisco Peninsula and southern Marin with the two taxa from the Monterey and San Simeon area, creating his *Arctostaphylos hookeri* complex. *Arctostaphylos hookeri* subsp. *montana* (Eastw.) Wells and *A. hookeri* subsp. *ravenii* are both tetraploid, serpentine endemic species. While some similarities exist, they differ from *A. hookeri* subsp. *hookeri* in a number of characters, but principally with regard to the nascent inflorescences and fruit. Morphologically similar to the two serpentine endemics is the diploid, *A. hookeri* subsp. *franciscana* (Eastw.) Munz, also a serpentine endemic, but extirpated in the wild. *Arctostaphylos hookeri* subsp. *hookeri* is a diploid endemic to the Monterey region and is found on sandy or clay soils. *Arctostaphylos hookeri* subsp. *hearstiorum* (Hoover & Roof) Wells is a diminutive taxon, similar in structures to *A. hookeri* subsp. *hookeri*, but much smaller; the plant is also completely prostrate, and is found in grazed grassland areas on mostly clay soils.

Markos et al. (1999) examined this group using molecular markers, principally from the nuclear ribosomal ITS region. The result was that the three northern taxa, *A. hookeri* subsp. *montana*, *A. hookeri* subsp. *franciscana*, and *A. hookeri* subsp. *ravenii*, were not closely related to the two more southerly distributed subspecies, *A. hookeri* subsp. *hookeri* and *A. hookeri* subsp. *hearstiorum*. These results have been substantiated in later work with more species (Boykin et al. 2005; Wahlert 2005), and supports separation of the northern taxa from *A. hookeri*. As a result, we propose to resurrect *A. franciscana* and *A. montana* at species rank and to make a new combination for subsp. *ravenii*. We provide the following treatment and key to this revised complex:

Arctostaphylos montana Eastw. subsp. **ravenii** (P. V. Wells) V. T. Parker, M. C. Vasey, J. E. Keeley, comb. nov.—*Arctostaphylos hookeri* subsp. *ravenii* P. V. Wells, Madroño 19: 200, 1968. Type: USA, California, San Francisco Co., on serpentinite in the Presidio, *P. V. Wells 2767* (holotype UC).

KEY FOR THE FORMER *ARCTOSTAPHYLOS HOOKERI* COMPLEX:

1. Immature inflorescence inconspicuous, small, often dark raceme (rarely with one branch), leaves shiny green, elliptic to diamond-shaped (*A. hookeri*)
   2. Plants generally erect shrubs (>0.5 m in height), leaves narrowly to broadly elliptic, 2–3 cm L, 1–1.5 cm W . . . . *A. hookeri* subsp. *hookeri*
   2′ Plants strongly prostrate shrubs (<0.25 m in height), leaves), narrowly elliptic to diamond-shaped, quite small (0.8–1.2 cm L; 0.4–0.7 cm W) . . . . *A. hookeri* subsp. *hearstiorum*

1′ Immature inflorescence prominent and conspicuous, congested umble or panicle usually with several branches, leaves dull green, obovate to round-elliptic
   3. Fruits generally 6–8 mm wide, habit variable (may be erect), leaves not orbicular
      4. Leaves round-elliptic, 1–2.5 cm L, 1–2 cm W, young twigs white tomentose . . . . *A. montana* subsp. *montana*
      4′ Leaves narrow elliptic, 1.5–2 cm L, 0.5–1 cm W, young branchlets gray tomentose. . . . . *A. franciscana*
   3′ Fruits generally 4–5 mm wide, plants always prostrate, leaves orbicular, 1–2 cm L, 1–1.5 cm W . . . . *A. montana* subsp. *ravenii*

THE ARCTOSTAPHYLOS TOMENTOSA COMPLEX

Wells' (1987) vision that the *Arctostaphylos tomentosa* (Pursh) Lindl. complex is the core ancestral group of taxa in *Arctostaphylos* is based on several characters relatively atypical in the genus, such as bifacial leaves, leafy bracts, shreddy persistent bark, and resprouting ability, which are mostly shared among outgroup sister genera in the subfamily Arbutoideae (e.g., *Arbutus*, *Comorostaphylis*, *Xylococcus*, *Ornithostaphylos*, and *Arctous*), and consequently these characters are hypothetically basal within *Arctostaphylos*. However, whereas bifacial leaves and resprouting ability are shared among these other closely related genera, they are in general characterized by scaley bracts (not leafy) and at least three genera have members with smooth bark rather than persistent shreddy bark (i.e., *Arbutus*, *Ornithostaphylos*, and *Arctous*). Further, *A. tomentosa* taxa are all tetraploid in a genus dominated by diploid species and a more parsimonious hypothesis is that they are derivative rather than ancestral, even though containing a cluster of potentially ancestral characters. These taxa have probably resulted from hybridization between more basal diploid species. One model is that they are allopolyploids that originated from crosses similar to the documented origin of *A. mewukka* Merriam (Schierenbeck et al. 1992).

In our view, Wells also did not adequately consider the pattern and range of variation within this complex. He weighted very heavily the presence of a basal burl and bifacial leaves with few or no stomata on the upper surface, traits that are found in all taxa within the complex. But, he did not give adequate weight to the fact that different subspecies vary markedly with

respect to bark characteristics of the older stems: some have grey shreddy bark and others have smooth red bark. In addition, his typological concept of this complex also did not adequately appreciate the extent of population variation in other characteristics; for example, he asserted that leafy bracts associated with the nascent inflorescences were similar throughout the complex. Our studies fail to support Wells' view as we have observed that bract characteristics, although commonly consistent across populations of other species in the genus, exhibit extraordinary variation within these tetraploid species. Our studies reveal that those subspecies with red, smooth bark tend to have most, but not all, populations displaying smaller scale-like bracts, while those with shreddy bark tend to have most populations with leafy bracts. These inconsistencies have provided considerable confusion in the field for identifying these taxa.

We propose that dividing Wells' *A. tomentosa* complex into two species complexes, one group of taxa with grey, shreddy bark and another with red, smooth bark, yields a taxonomy that reflects population patterns with geographic continuity suggestive of more logical phylogenetic relationships. The gray, shreddy bark taxa comprise one cluster that is restricted to the Monterey region and sparingly down the coast to San Luis Obispo County. The red, smooth barked taxa form another group that dominates the Santa Cruz Mountains, ridges of the east side of San Francisco Bay, inland to Mt. Diablo, south into the Gabilan Mountains, and north to southern Napa County. The latter complex is also distributed in isolated populations from Monterey to Santa Barbara Counties, and on the Channel Islands.

Based on the type specimen, the name *A. tomentosa* (Pursh) Lindl. (Pursh 1814; Lindley 1836) rightly belongs to the grey, shreddy bark group in this complex. Young twigs on *A. tomentosa* are short hairy, with similar hair on the lower surface of the leaves, often thinning with age. On subsp. *bracteosa* (DC.) Adams, twigs are also short hairy, and differ from subsp. *tomentosa* by also having long gland-tipped bristles, sparsely so on the lower surface of the leaves. Another population of a member of the *A. tomentosa* complex can be found in Monterey County, subsp. *hebeclada*, originally considered by DeCandolle (1839) as a variety of *Andromeda bracteosa* (treated here as subsp. *bracteosa*); these populations were treated at a level below subspecies by Wells. Eastwood (1934) classified it as a variety of *Arctostaphylos bracteosa*, while later McMinn (1939) named it a variety of *A. tomentosa*. Although distinctively glabrous on its lower leaf surfaces and lacking glandular bristles, this taxon was submerged in the Jepson treatment by Wells (1993). Twigs are sparsely short hairy. Aside from its gray, shreddy bark, it is very similar to *A. crustacea* ssp. *rosei*. Separating the *A. tomentosa* and *A. crustacea* complexes provides the opportunity to effectively distinguish between these two taxa. Populations of subsp. *tomentosa*, subsp. *bracteosa*, and subsp. *hebeclada* are all restricted to Monterey County, from Fort Ord to Carmel Valley, with subsp. *tomentosa* sparingly found farther south down the coast. The final member of the *A. tomentosa* complex is subsp. *daciticola* P.V. Wells, only found near Morro Bay on the volcanic peaks inland a few kilometers. Twigs are short hairy but also have longer non-glandular, white bristles. Lower leaf surface is tomentose to smooth with age.

Arctostaphylos tomentosa (Pursh) Lindl. subsp. **hebeclada** (DC.) V. T. Parker, M. C. Vasey and J. E. Keeley, comb. nov.—*Andromeda bracteosa* DC. var. *hebeclada* DC., Prodr. 7(2): 607, 1839. *Arctostaphylos bracteosa* DC. var. *hebeclada* (DC.) Eastw. Leafl. W. Bot. 1:122. 1934. *Arctostaphylos tomentosa* (Pursh) Lindl. var. *hebeclada* (DC.) J. E. Adams ex McMinn. Man. Calif. Shrubs, 412. 1939. Type: USA, "Nova California", *Douglas 1524* (G-DC).

The red, smooth bark group includes two taxa named in the same early publication by Eastwood (1933), *A. crustacea* Eastw. and *A. rosei* Eastw. We have chosen the former taxon because of its priority within the publication. *Arctostaphylos crustacea* also has a wider distribution; Eastwood's description was originally based on specimens from the San Francisco area, Moraga Ridge and Grizzly Peak in the eastern side of the San Francisco Bay, and various places in the Santa Cruz Mountains. Twigs on this taxon are short hairy with long bristles, sometimes with glands on the bristles. The lower leaf surface is sparsely hairy but thins with age. This subspecies is distributed from southern Napa County, the hills on the east side of SF Bay over to Mt. Diablo and south to the Gabilan Mountains. It is also found throughout the Santa Cruz Mountains south to Monterey. Isolated populations range near the coast to the Channel Islands. Subspecies *rosei* differs by having twigs that are short hairy while leaf surfaces are smooth and glabrous. Flower pedicels and ovary are tomentose. Several small populations of this taxon occur along the Big Sur coast, however, the type locality is from the dunes of western San Francisco, now reduced to two known individuals.

An additional member of this complex is subsp. *crinita*. Some taxonomic confusion has existed with the name of this taxon. McMinn (1939) used this name based on Adams' dissertation, but later Adams (1940) called it *Arctostaphylos crustacea* var. *tomentosiformis*. Wells

(1968) originally followed Adams and used the subspecific name *tomentosiformis*, but in a later treatment (Wells 1987), following clarification by Gankin (1971), Wells switched to *A. tomentosa* subsp. *crinita*. This taxon is quite similar to *A. crustacea*, except that it is densely hairy on the lower surface of the leaves, and even sometimes is hairy on the upper surface as well. Its distribution is primarily in the southern Santa Cruz Mountains.

Three subspecies are found in southern California. Narrowly restricted to the Purissima Hills north of Lompoc in Santa Barbara County is subsp. *eastwoodiana*, associated with an outlying population of *Pinus muricata*. While the twigs on this plant are sparsely short hairy, leaf blades are smooth and glabrous, as is the pedicel and ovary. Although morphologically similar to subspecies *rosei*, in subsp. *eastwoodiana* the ovary is glabrous, while tomentose in subsp. *rosei*. Generally restricted to Santa Rosa and Santa Cruz islands is subsp. *insulicola*, although some individuals have been found in the southern Santa Cruz Mountains as well. Twigs are generally short hairy and leaves sparsely tomentose on the lower surface. Subspecies *subcordata* is another taxon restricted to Santa Cruz and Santa Rosa Islands. Twigs petioles, rachises and bracts are densely glandular hairy, often with longer glandular hairs.

Resurrecting *A. crustacea* requires a change in the names of many of the subspecific taxa, and here we provide an accounting of those taxa separated into *A. crustacea*, as well as a key to distinguish among the subspecies of both *A. tomentosa* and *A. crustacea*.

Arctostaphylos crustacea Eastw. subsp. **crinita** V. T. Parker, M. C. Vasey and J. E. Keeley, comb. nov.—*Arctostaphylos tomentosa* (Pursh) Lindl. var. *crinita* Adams ex McMinn, Man. Calif. Shrubs, 412, 1939. *Arctostaphylos crustacea* Eastw. var. *tomentosiformis* J. E. Adams, J. Elisha Mitchell Sci. Soc. 56: 54. 1940. *Arctostaphylos tomentosa* (Pursh) Lindl. var. *tomentosiformis* (J. E. Adams) Munz, Aliso 4: 95. 1958. *Arctostaphylos tomentosa* (Pursh) Lindl. subsp. *tomentosiformis* (J. E. Adams) P. V. Wells, Madroño 19: 198. 1968. *Arctostaphylos tomentosa* (Pursh) Lindl. subsp. *crinita* (J. E. Adams) Gankin, Madroño 21: 148. 1971.—Type: USA, California, Santa Cruz Co., Bonny Doon Ridge, head of Liddell Creek, *J. E. Adams 928* (holotype UC).

Arctostaphylos crustacea Eastw. subsp. **eastwoodiana** (P. V. Wells) V. T. Parker, M. C. Vasey and J. E. Keeley, comb. nov.—*Arctostaphylos tomentosa* (Pursh) Lindl. subsp. *eastwoodiana* P. V. Wells, Madroño 19:197. 1968.—Type: USA, California, Santa Barbara Co., on diatomite, summit of La Purissima Ridge, *P. V. Wells 610672* (holotype UC).

Arctostaphylos crustacea Eastw. subsp. **insulicola** (P. V. Wells) V. T. Parker, M. C. Vasey and J. E. Keeley, comb. nov.—*Arctostaphylos tomentosa* (Pursh) Lindl. subsp. *insulicola* P.V. Wells, Madroño 19:197. 1968.—Type: USA, California, basaltic rocks above Pelican Bay, Santa Cruz Island, *P. V. Wells and J. B. Roof 5467*, (holotype UC).

Arctostaphylos crustacea Eastw. subsp. **rosei** (Eastw.) V. T. Parker, M. C. Vasey and J. E. Keeley, comb. nov.—*Arctostaphylos rosei* Eastw., Leafl. W. Bot. 1:77. 1933. *Arctostaphylos tomentosa* (Pursh) Lindl. subsp. *rosei* (Eastw.) P. V. Wells, Madroño 19: 198. 1968.—Type: USA, California, San Francisco Co., on the hills bordering Lake Merced, *L. S. Rose 33037* (holotype CAS).

Arctostaphylos crustacea Eastw. subsp. **subcordata** (Eastw.) V. T. Parker, M. C. Vasey and J. E. Keeley, comb. nov.—*Arctostaphylos subcordata* Eastwood, Leafl. W. Bot. 1:61, 1933. *Arctostaphylos tomentosa* (Pursh) Lindl. subsp. *subcordata* (Eastw.) P. V. Wells, Madroño 19: 198. 1968.—Type: USA, California, Santa Barbara Co., Santa Cruz Island, *J. T. Howell 6335* (holotype CAS).

KEY FOR THE *ARCTOSTAPHYLOS TOMENTOSA/A. CRUSTACEA* COMPLEX OF ERECT PLANTS WITH PROMINENT BURLS, BEARING STOMATA ONLY ON THE LOWER SURFACE OF THE LEAVES:

1. Lower stems grey, shreddy barked
    2. Twigs densely short pubescent with long glandular bristles . . . . *A. tomentosa* subsp. *bracteosa*
    2′ Twigs densely pubscent but lacking long bristles with glands
        3. Twigs with long bristles above a short pubescence . . . . *A. tomentosa* subsp. *daciticola*
        3′ Twigs lacking long bristles above short, dense pubescence
            4. Lower leaf surfaces densely pubescent . . . . *A. tomentosa* subsp. *tomentosa*
            4′ Lower leaf surfaces glabrous or sparsely pubescent. . . . . *A. tomentosa* subsp. *hebeclada*

1′ Lower stems smooth, reddish barked
    5. Twigs with dense short pubescence and long glandular bristles . . . . *A. crustacea* subsp. *subcordata*
    5′ Twigs with dense short pubescence but generally lacking long glandular bristles
        6. Twigs with long, non-glandular bristles above a short pubescence
            7. Lower leaf surfaces glabrous or sparsely pubescent. . . . . *A. crustacea* subsp. *crustacea*

7′ Lower leaf surfaces densely pubescent, sometimes less so on upper side . . . . *A. crustacea* subsp. *crinita*

6′ Twigs with dense short pubescence, lacking long bristles

8. Lower surface of leaves glabrous

9. Pedicels and ovary short hairy . . . . *A. crustacea* subsp. *rosei*

9′ Pedicels and ovary glabrous . . . . *A. crustacea* subsp. *eastwoodiana*

8′ Lower surface of leaves persistently short hairy . . . . *A. crustacea* subsp. *insulicola*

Other Considerations of the Current Jepson Manual Treatment

Further changes expected in the upcoming Jepson treatment include the following observations: Revision of the *A. glandulosa* subspecies (Keeley et al. 2007); range extension and addition of two burl-forming subspecies of *A. parryana* (Keeley et al. 1997b); removal of *A. peninsularis* Wells (from the state and inclusion of *A. rainbowensis* Keeley and Massihi [1994]); inclusion of *A. gabilanensis* (Parker and Vasey 2004), a new species from the southern Santa Cruz Mountains and a new subspecies of *A. patula* from the Sierra Nevada (Vasey and Parker in review). We also propose 3 additional revisions that follow.

When Wells (1968) published a new subspecies of *A. pilosula* Jeps., viz. *A. pilosula* subsp. *pismoensis* Wells, his description of *A. pilosula* subsp. *pismoensis* was of plants with leaves greener and more elliptic than those of the nominate subspecies from the type locality. Later, Knight (1989) changed the status and name of *A. pilosula* subsp. *pismoensis* to *A. wellsii* Knight. In Knight's article, he asserted that *A. wellsii* differs from *A. pilosula* in 17 morphological features that he listed. We examined the types of both *A. pilosula* (*A. E. Wieslander 552*, holotype UC) and A. *pilosula* subsp. *pismoensis* (*P. V. Wells 23*, holotype UC; cited as the type for *A. wellsii* in Knight [1989]), as well as a number of additional collections from the Atascadero region, Pozo Summit, Pismo Beach area, and sites inland. Patterns of variation and similarity among these collections calls into question the distinction between these taxa. A major problem is that most of the characters listed by Knight (1989) for *A. wellsii* actually better describe the type specimen for *A. pilosula*, specifically, twig, rachis and petiole hispidity, bract shape, density of ciliate hairs on bracts, and other characters. Other characters listed by Knight (1989) are quite variable among all populations, sometimes even within individuals, such as whether the filaments are glabrous or hairy at the base. In short, the characters used by Knight (1989) to segregate out *A. wellsii* do not differentiate collections from the type of *A. pilosula*. There are morphological trends, such as individuals with ovate to oblong-ovate leaves and much more glaucous hue being found at Pozo Summit, but on the whole, we find it difficult to separate these two taxa.

When the range of *A. pilosula* and *A. wellsii* as a whole is considered, plants in the northern part of the range at lower elevations (e.g., Atascadero to Santa Margarita) as well as in the southern part of the distribution (e.g., Price Canyon, areas around Huasna Road and Lopez Road) are essentially identical in morphology. Most individuals at Pozo Summit do appear to have rounder, whiter leaves, suggesting introgression with *A. glauca*, but numerous collections from either side of the summit demonstrate a mosaic of combinations, including individuals that would key out to *A. wellsii*. Strikingly, many collections at UC and JEPS from the Pozo Mountain region of *A. pilosula* are annotated by Knight with statements such as 'not typical for *A. pilosula*', and in those collections the leaves are more elliptic and greener than he perhaps was expecting for the location. Accordingly, we are submerging *A. pilosula* ssp. *pismoensis* and *A. wellsii* into *A. pilosula*.

Gankin and Hildreth (1988) published a new taxon from high elevation sites in the North Coast Ranges called *Arctostaphylos knightii* Gankin & Hildreth, a plant very similar to *A. nevadensis* except that it possessed burls and could resprout after fire. Wells (1988) transferred this taxon to subspecific status within *A. nevadensis*, but with his later treatments (Wells 1993, 2000) submerged it into *A. nevadensis*, considering it a hybrid. The considerable range of this taxon, and its large populations in some areas requires reconsideration. On the serpentinized peridotite areas at the California-Oregon border that were burned in the Biscuit Fire in 2002, for example, an extensive population of *A. nevadensis* subsp. *knightii* is resprouting and reestablishing its population. This population was throughout the areas we visited in Del Norte County, which makes it difficult to imagine this as an occasional hybrid between two parents, one of which does not occur at that elevation. Consequently, we recognize this subspecies as a valid entity as a subspecies of *Arctostaphylos nevadensis*.

Another entity deserving more attention is *Arctostaphylos pacifica* Roof, a burl-sprouting prostrate plant found on San Bruno Mountain in San Mateo County described by Roof (1962). This plant has been relegated to hybrid status by Wells (1993, 2000) within his treatment of *A. uva-ursi*. The problem with that hypothesis is that the presence of one parent on San Bruno Mountain, *A. glandulosa*, cannot be confirmed. We have

collected specimens from all the large burl-formers on San Bruno Mountain, and they represent good examples of *Arctostaphylos crustacea* subsp. *crustacea*, (with some glandulosity on several individuals). Among our collections, only two individuals of *A. crustacea* have any stomata on the upper surface and the density is considerably less than that of the lower surface. *Arctostaphylos pacifica*, however, is isofacial in stomatal density, as well as having a burl and a unique leaf condition (serrulate margins) among mature leaves; these characters do not support a hybrid origin for *A. pacifica* between *A. uva-ursi* and another San Bruno Mountain manzanita unless the characters are transgressive. Determining the chromosomal count of this taxon would be an initial first step toward understanding its relationships. However, given its distinct suite of characters and the unlikely assumption that it is a local hybrid (between parents currently in the vicinity), we resurrect this taxon as a valid species.

Other studies are ongoing for this complex genus and additional changes might be expected in the future. A number of plants have disappeared in more recent treatments, for example, because they have been considered hybrids, generally without any evidence being provided. Most of these we think deserve more investigation, such as a plant described by Howell (1945) as *Arctostaphylos cushingiana* Eastw. forma *repens* J. T. Howell. In Howell's article, he describes the near prostrate habit of this plant being *A. cushingiana* selected by ecological conditions of the habitat and even specifically dismisses the possibility of hybridization. Later, in a table of chromosome counts in the genus, Wells (1968) classified forma *repens* as a hybrid form indicating his interpretation that Howell bases his name on hybrid individuals. In his later treatments, he includes *A.* × *repens* within his treatment of *A. uva-ursi*, in contrast to Howell's interpretation (e.g., Wells 2000) of forma *repens* being derivative of *A. cushingiana* (*A. glandulosa* subsp. *cushingiana*). What strikes us as most incredible about the taxonomic shuffling of Howell's forma *repens*, is that Wells (1968) provides a diploid chromosome count for it, even though he describes it as of hybrid origin from two tetraploid parents; we know of no reasonable genetic process by which this could happen. We are in the process of re-examining the ploidy level of this entity. If it is in fact a diploid, then it could well represent a distinct entity worthy of taxonomic recognition.

Other complexes require additional attention in the future. Two obvious ones are the *A. uva-ursi* complex and the *A. manzanita* complex. Recent work suggests that many of the characters in *A. uva-ursi* are variable and not taxonomically informative (Rosatti 1987), and some molecular work indicates the close relationship among the various populations (Wahlert 2005). Its widespread distribution and patterns of morphology and ploidy levels suggest an interesting history that deserves more attention. Similarly, the *A. manzanita* complex is widespread and variable within California. Any new treatment of these complexes will require a better understanding of evolutionary relationships among their taxa and the role of hybridization in their origin.

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NEW MORPHOLOGICAL MEASUREMENTS OF *PSITTACANTHUS ANGUSTIFOLIUS* AND *PSITTACANTHUS PINICOLA* (LORANTHACEAE)

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ABSTRACT

Additional measurements of leaves and flowers are reported for *Psittacanthus angustifolius* and *P. pinicola* from Central America and southern Mexico. Measurements for mature fruits and seeds of *P. angustifolius* are reported for the first time. Additional information on the phenology, host range, and distribution of these mistletoes is also reported.

RESUMEN

Se reportan mediciones adicionales de hojas y flores de *Psittacanthus angustifolius* y *P. pinicola* en Central América y el México del sur. Mediciones de los frutos maduros y las semillas de *P. angustifolius* están reportadas por primera vez. Información adicional sobre la floración, rango de hospederos y distribución de las dichas muérdagos también están reportadas.

Key Words: Central America, Mexico, mistletoes, pines, *Pinus*.

Psittacanthus angustifolius Kuijt and *Psittacanthus pinicola* Kuijt (Loranthaceae) were not described until 1987 from northwestern Nicaragua and central Belize, respectively (Kuijt 1987). These mistletoes are the most common loranthaceous species parasitizing pines in Central America (Mathiasen et al. 2003). They occur on several species of pines (Table 1), but *P. angustifolius* has also been reported on a wild guava (*Psidium guineense* Sw.) in Honduras and on oaks (*Quercus* spp.) in Chiapas, Mexico (Melgar et al. 2001). Thus far, *P. pinicola* has only been reported to parasitize pines (Kuijt 1987; Mathiasen et al. 2003).

Although both mistletoes commonly parasitize pines, they are clearly distinct species (Kuijt 1987). *Psittacanthus angustifolius* has much longer and thinner leaves than *P. pinicola* and its leaves are usually falcate and opposite; whereas leaves of *P. pinicola* are usually whorled and symmetrical. The inflorescences of *P. angustifolius* are terminal and the flowers are produced in triads, while the inflorescences of *P. pinicola* are lateral and the flowers are in dyads. According to Kuijt's original descriptions, the petals of *P. angustifolius* are approximately 8 cm long and bright orange, but those of *P. pinicola* are only 4 cm in length and consistently red with green tips. Other distinguishing characteristics include a distinct, fleshy, ligule-like median crest extending inwards at the top of each petal of *P. angustifolius* and a distinct ligule at the base of each petal of *P. pinicola*. Kuijt (1987) provided excellent line drawings of both taxa (see his Figures 10, 12, and 13).

Even though both of these mistletoes commonly parasitize pines in Central America and *Psittacanthus angustifolius* is associated with mortality and growth loss of economically important species, no additional morphological studies have been completed on these mistletoes since Kuijt's original descriptions. Kuijt (1987) based his description of *P. angustifolius* on only two collections from the same location in Nicaragua and used seven collections as the basis for his description of *P. pinicola*. Therefore, we

TABLE 1. HOST RANGE OF *PSITTACANTHUS ANGUSTIFOLIUS* AND *P. PINICOLA* IN CENTRAL AMERICA AND MEXICO (BZ—BELIZE; ES—EL SALVADOR; GT—GUATEMALA; HN—HONDURAS; NI—NICARAGUA). The classification of *Pinus* is based on Farjon and Styles (1997). The report of infection of *Quercus* spp. by *P. angustifolius* is from an unpublished monograph of the genus *Psittacanthus* in Central America by J. Kuijt.

	Central America	Country	Chiapas, Mexico
Psittacanthus angustifolius	*Pinus caribaea* var. *hondurensis*	HN, NI	*Pinus oocarpa* *Pinus maximinoi*
	Pinus maximinoi	HN	*Pinus tecunumanii*
	Pinus oocarpa	ES, GT, HN, NI	*Quercus* sp.
	Pinus tecunumanii	HN, NI	
	Psidium guineense	HN	
Psittacanthus pinicola	*Pinus caribaea* var. *hondurensis*	BZ, HN, NI	
	Pinus oocarpa	HN, NI	
	Pinus tecunumanii	BZ, NI	

have been collecting additional measurements of key morphological characters since 1999 from throughout Central America for both species and from Chiapas, Mexico, for *P. angustifolius*. Here we report the results of our work, which includes the first measurements of mature fruits and seeds of *P. angustifolius*. We also report additional information on the phenology, host range, and distribution of these mistletoes based on recently completed surveys in Guatemala, Honduras, Nicaragua, and Chiapas, Mexico.

METHODS

Mature leaves were measured from 22 populations of *P. angustifolius* (Fig. 1, populations 1–3, 6, 10–14, 16, 18, 20–26, 30–32, and 36) and from 12 populations of *P. pinicola* (Fig. 2, populations 1, 3–6, 8, 9, and 11–15) sampled from 1998 through 2006. Mature flowers were measured from 13 populations of *P. angustifolius* (Fig. 1, populations 4, 7, 12, 13, 14, 16, 20, 21, 23–26, and 31) and 8 populations of *P. pinicola* (Fig. 2, populations 3, 5, 6, 9, 11, 12, 14, and 15). Mature fruits and seeds were measured for 5 populations of *P. angustifolius* (Fig. 1, populations 2, 5, 10, 16, and 23) and for 7 populations of *P. pinicola* (Fig. 2, populations 3, 5, 6, 9, 11, 12, and 14). Some measurements of leaves (15 total) were made from three herbarium specimens for *P. pinicola* (Fig. 2, populations 17–19), but no measurements of floral or fruit characters were made using herbarium specimens because of shrinkage associated with drying.

Herbarium specimens provided additional information on the distribution of both taxa in Central America. All of the herbarium specimens we examined for species of *Psittacanthus* reported on pines from Central America were either *P. angustifolius* or *P. pinicola*, although many of these collections had been classified as *Psittacanthus schiedeanus* (Cham. & Schlecht.) Blume. Most early reports from Central America of *Psittacanthus* on pines were attributed to *P. schiedeanus* because *P. angustifolius* and *P. pinicola* were not described until 1987 (Kuijt 1987; Mathiasen et al. 2003). We examined specimens of *P. angustifolius* at the following herbaria: EAP, UVAL, TEFH, HNMN, and specimens of *P. pinicola* at: EAP and HNMN. Voucher specimens of *P. angustifolius* and/or *P. pinicola* have been deposited at ASC, EAP, UVAL, HNMN, or at the Herbario, Escuela National de Ciencias Forestales, Siguatepeque, Honduras, C.A.

Morphological characters measured included: leaves—length and width, petiole length, and shape of the leaf, leaf apex and base; inflorescences—length of peduncles and pedicels, length and width of the base of mature buds, length and width of individual petals, length of anthers, length of filaments, and the distance from the base of petals to the point of attachment of the filaments, length and width of ovaries, and length of styles; fruits—length, width, and color; seeds—length, width, color, and number of cotyledons. For each sampled population, measurements were made for each character from ten randomly selected mature leaves, flowers, and fruits. Leaves were sampled from the lower part of plants to assure they were fully developed. Only flowers that had opened and fruits that were dark purple were considered mature. Measurements were made with a Plasti-cal digital caliper accurate to 0.1 cm or a Bausch and Lomb 7× hand lens equipped with a micrometer accurate to 0.1 mm.

MEASUREMENTS OF LEAF AND FLOWER CHARACTERS

Measurements of leaf and flower characters for *Psittacanthus angustifolius* and *P. pinicola* are summarized in Table 2. Leaf sizes (length and width) were larger than those reported by Kuijt (1987) for both taxa. Kuijt reported that leaves of *P. angustifolius* were 17 × 2.5 cm. We found plants of *P. angustifolius* with leaves up to 26 cm in length and 6 cm in width, but leaf length and width were not correlated in that long leaves (>20 cm) were often 2–3 cm in width. In general,

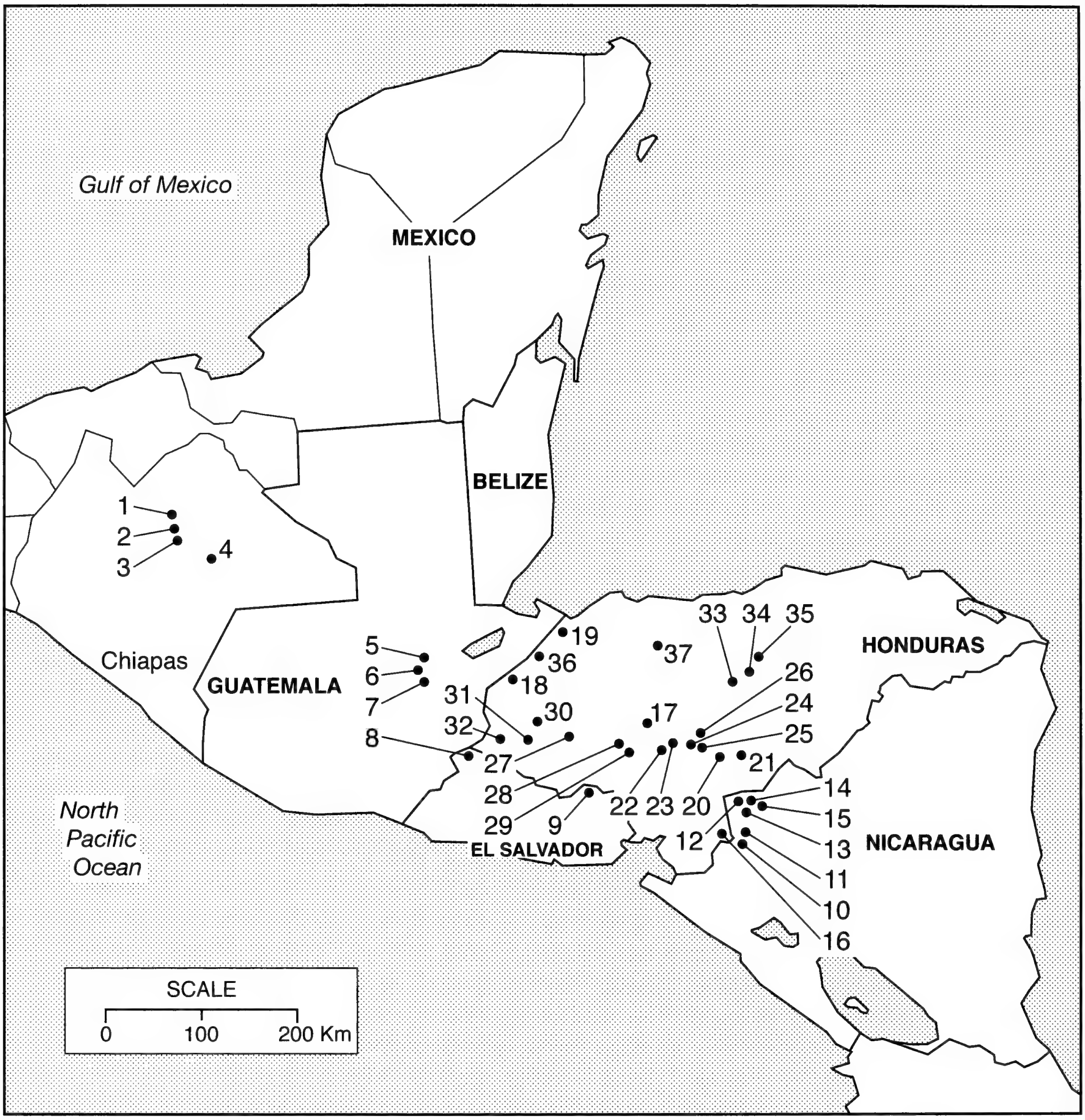

FIG. 1. Distribution of *Psittacanthus angustifolius* in Central America and Mexico based on collections and reports. See text for listing of populations used for leaf measurements, floral measurements, and fruit measurements. All populations on *Pinus oocarpa*, except as noted. MEXICO: Chiapas. **1**—1.2 km south of Pueblo Nuevo on Route 195; **2**—3.3 km north of Jitotol on Route 195; **3**—4 km south of Jitotol on Route 195, on *Pinus tecunumanii*; **4**—11.6 km east of the junction of Route 186 and the road to Altamarano on Route 186, ca. 8 km south of Ocosingo, on *Pinus maximinoi*. GUATEMALA: Department Baja Verapaz. **5**—1 km east of Santa Bárbara; **6**—6 km south of La Cumbre near Los Ramones on highway CA-14; **7**—16 km south of La Cumbre on highway CA-14; EL SALVADOR: Department Santa Anna. **8**—Monte Cristo National Park, ca. 12 km east of the park headquarters; Department Morazan. **9**—On the road from Sabanetas, Honduras to Perquin, El Salvador; NICARAGUA: Department Madriz. **10**—0.5 km south of San Jose de Cusmapa; **11**—3 km north of San Jose de Cusmapa on road to Somoto; Department Nueva Segovia. **12**—4.3 km north of highway NIC-29 on road to Bayuncun; **13**—4.3 km north of Mozonte; **14**—8.4 km north of Mozonte; **15**—5.1 km north of Sabana Grande, on *Pinus caribaea* var. *hondurensis*; HONDURAS. Department Choluteca. **16**—10 km east of San Marcos de Colón near border with Nicaragua; Department Comayagua. **17**—8 km southeast of Siguatepeque; Department Copan. **18**—21 km from highway CA-4 on road to San Agustín; Department Cortes. **19**—15 km northwest of Cofradia on road to Buenos Aires; Department El Paraiso. **20**—5 km southeast of Yuscaran; **21**—0.7 km north of the road to Potrerillos on highway CA-6; Department Francisco Morazan. **22**—1 km southwest of Lepaterique; **23**—4 km east of Lepaterique on road to Tegucigalpa; **24**—2 km east of the main road to Tegucigalpa on road to Tatumbla; **25**—6.5 km north of Zamorano on highway to Tegucigalpa; **26**—7.4 km south of Valle de Angeles on road to

mature leaf length and width were extremely variable, even on the same *P. angustifolius* plant. Leaves of *P. angustifolius* were usually falcate, sometimes strikingly so, but some leaves were straight and symmetrical. The long, narrow, falcate leaves of *P. angustifolius* were indicative of this species and could usually be used to identify this mistletoe on trees, even at some distance. Leaf apexes were typically acuminate, but some leaves had rounded apexes. Leaf bases were attenuate to acute with no clear petiole attached to the stem or with petioles of varying lengths up to 7 mm. Kuijt (1987) indicated that leaves of *P. pinicola* were 11×2.5 cm. We found that leaves were as long as 13 cm and to 7.5 cm in width. The leaves of *P. pinicola* were usually arranged in what Kuijt (1987) referred to as "irregular whorls"; their points of attachment were slightly offset from each node. However, we will refer to the leaves as being in a whorled arrangement. Mature leaves were consistently symmetrical with rounded to acuminate apexes. The leaf base tapered to the petiole which was up to 9 mm in length. The leaves of *P. pinicola* were thick (approximately 0.9–1.2 mm) and leathery in texture, while the leaves of *P. angustifolius* were thin (approximately 0.5–0.7 mm) and pliable. In general, the shape, length, and width of the mature leaves of *P. pinicola* were much less variable than those of *P. angustifolius*. Leaf arrangement (opposite vs. whorled), shape (falcate vs symmetrical), and leaf texture (thin and pliable vs. thick and leathery) would usually distinguish these taxa if flowers and fruits were not available.

On average, the length of petals for both taxa were similar to what Kuijt (1987) reported. But it should be noted that flowers were generally larger for *P. angustifolius* from Honduras than originally described by Kuijt (9–11 vs. about 8 cm). Our measurements from Nicaragua indicated that most of the floral characters of *P. angustifolius* were smaller there. For example, petals of *P. angustifolius* from Honduras averaged 9.6 cm and 1.6 mm in length and width, respectively, but they only averaged 7.3 cm and 1.1 mm from Nicaragua. So our measurements agree with Kuijt's original description of *P. angustifolius*, which used flowers collected from northwestern Nicaragua.

Our measurements of floral pedicels and peduncles were similar to those reported by Kuijt for both species, but we found that the length of the foliaceous bract often associated with the lower triads of *P. angustifolius* may be as long as 5.5 cm. However, usually this foliaceous bract was much shorter or even absent. *Psittacanthus pinicola* does not have a foliacious bract.

Kuijt reported an anther length of 6 mm for *P. angustifolius*, but the average anther length we measured was only 4.4 mm and only the largest anthers were around 6 mm in length. The anther length for *P. pinicola* varied from 3.6 to 4.2 mm; Kuijt reported the anther length was from 3–4 mm. The length of filaments (from the point of attachment on petals to anthers) averaged 3.8 cm for *P. angustifolius*, which is much shorter than the filament length reported by Kuijt (5 cm). Only the longest filaments we observed were around 5 cm long. The length of filaments of *P. pinicola* averaged 1.5 cm and this is the same length reported by Kuijt. Our measurements of the distance from the base of petals to the point of filament attachment averaged 3.8 cm for *P. angustifolius*, differing from Kuijt's of 2.5 cm. Our measurements from Nicaraguan populations were similar to those reported by Kuijt for this character.

The average ovary lengths based on our measurements were approximately the same as what Kuijt reported for both species. But our measurements of ovary width (mean 2.7 mm) were larger than what Kuijt (2 mm) found for *P. pinicola* and smaller (mean 4.3 mm) than what he reported for *P. angustifolius* (5 mm). The length of styles of *P. angustifolius* averaged 7.6 cm; Kuijt did not report information for this character. Our measurements of the styles of *P. pinicola* were much shorter (3.5 cm) than that reported by Kuijt (4.6 cm). We also noted that the base of the style of *P. pinicola* was usually twisted, while it was straight for *P. angustifolius*.

Measurements of fruits and seeds for both taxa are summarized in Table 3. Our measurements of the fruits of *P. pinicola* are larger than what Kuijt reported and our measurements of mature fruits are the first reported for *P. angustifolius*. Seed sizes are the first reported for both taxa. Fruits of both species are initially green, gradually turn red, and are dark purple when mature. Seeds of *P. angustifolius* are dark green to brown while those of *P. pinicola* are consistently light green. The number of cotyledons in seeds varied from

←

Tegucigalpa; Department Intibuca. **27**—9 km north of Yamaranguila; Department La Paz. **28**—26 km west of junction with highway CA-5 on road to Marcala; **29**—1 km north of El Tejar, on *Pinus tecunumanii*; Department Lempira. **30**—1.3 km east of El Matazano on road to San Rafael, on *Pinus maximinoi*; **31**—5 km west of Gracias on road to Villa Verde; Department Ocotopeque. **32**—0.2 km east of the junction with the road to Pashapa on highway CA-4; Department Olancho. **33**—11 km northwest of Concordia; **34**—13 km south of Guiamaca; **35**—10 km east of Gualaco on road to San Esteban, on *Pinus caribaea* var. *hondurensis*; Department Santa Bárbara. **36**—4 km east of Pinalejo on road to Buenos Aires; Department Yoro. **37**—20 km north of Yoro on road to La Flores.

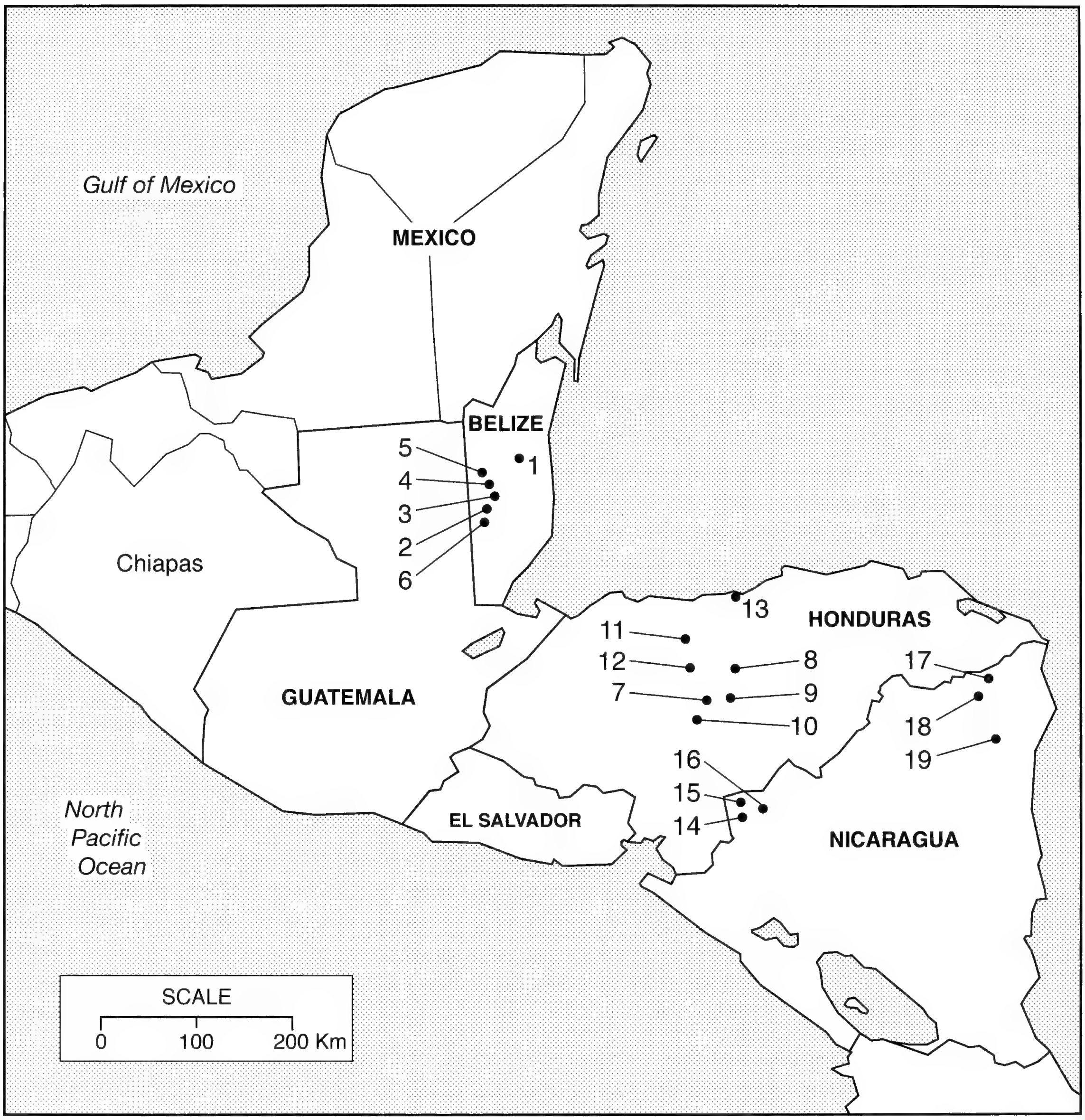

FIG. 2. Distribution of *Psittacanthus pinicola* in Central America based on collections. See text for listing of populations used for leaf measurements, floral measurements, and fruit measurements. All populations on *Pinus caribaea* var. *hondurensis*, except as noted. BELIZE: Belize District. **1**—Manatee Ridge near milepost 31 west of Belize City along the Western Highway (2 km west of the junction to Dangria); Cayo District. **2**—2.4 km south of Cooma Cairn Lookout on Cooma Cairn Road; **3**—1 km south of Cooma Cairn Lookout on Brunton Trail; **4**—0.5 km north of Cooma Cairn Lookout on Cooma Cairn Road; **5**—Junction of Dumbcane Trail and trail to Butterfly Falls, on *Pinus tecunumanii*; **6**—2.5 km south of Cooma Cairn on Brunson Trail; HONDURAS: Department Olancho. **7**—13 km northwest of Concordia; **8**—1.7 km southwest of El Carbon on road to San Esteban; **9**—22 km southwest of El Carbon on road to San Esteban; **10**—At km post 144 on main highway from Juticalpa to Tegucigalpa; Department Yoro. **11**—20 km north of Yoro on road to La Flores; **12**—25 km east of Yoro on the road to Olanchito; Department Colón. **13**—5.5 km east of the junction of the North Coast Highway and the road to Limon along the North Coast Highway; NICARAGUA: Department Nueva Segovia. **14**—4.3 km north of Highway NIC-29 on road to Bayuncun; **15**—7.5 km north of Highway NIC-29 on road to Bayuncun, on *Pinus tecunumanii*; **16**—4.5 km east of San Fernando on Highway NIC-29; Department Zelaya. **17**—Bilwaskarna; **18**—Rio Tranquera at junction with road between Waspam and Puerto Cabezas; **19**—near Tala Has and Puente Mango (over Rio Kisalaya).

TABLE 2. MORPHOLOGICAL CHARACTERISTICS OF THE LEAVES AND FLOWERS OF *PSITTACANTHUS ANGUSTIFOLIUS* AND *P. PINICOLA*. N/n represents the number of populations sampled over the number of individual measurements.

Characters measured	*P. angustifolius*				*P. pinicola*			
	Mean	Std. Dev.	Range	N/n	Mean	Std. Dev.	Range	N/n
Leaf length (cm)	13.8	3.8	6.3–26.1	22/220	8.3	1.5	5.1–13.0	15/135
Leaf width (cm)	2.4	1.0	0.7–6.2	22/220	3.1	1.2	1.0–7.5	15/135
Petiole length (mm)	2.5	1.5	0.0–7.0	22/220	5.6	1.8	0.0–9.0	15/135
Inflorescence peduncle length (mm)	1.3	0.3	0.7–2.0	13/130	0.7	0.2	0.4–1.3	8/80
Diad peduncle length (mm)	N/A	N/A	N/A	N/A	1.0	0.3	0.5–1.6	8/80
Flower pedicle length (mm)	1.7	0.4	0.9–2.8	13/130	0.6	0.1	0.4–0.8	8/80
Foliar bract length (cm)	2.9	1.4	0.8–5.5	13/130	N/A	N/A	N/A	N/A
Bud length (cm)	8.3	1.6	4.8–10.9	13/130	3.6	0.3	3.1–4.4	8/80
Bud base width (mm)	4.2	0.7	2.8–5.6	13/130	3.4	0.3	2.8–4.1	8/80
Petal length (cm)	8.7	1.4	5.8–11.2	13/130	3.8	0.3	3.1–4.4	8/80
Petal width (mm)	1.4	0.3	0.6–2.1	13/130	1.1	0.2	0.6–1.7	8/80
Filament length (cm)	3.8	0.8	1.6–5.1	13/130	1.5	0.1	1.2–1.7	8/80
Attachment of filament length (cm)	3.6	0.8	2.2–4.7	13/130	1.8	0.3	1.3–2.5	8/80
Anther length (mm)	4.4	1.1	2.1–6.1	13/130	3.9	0.2	3.6–4.2	8/80
Ovary length (mm)	6.2	1.5	3.3–10.3	13/130	4.3	0.6	3.3–5.9	8/80
Ovary width (mm)	4.3	1.0	2.4–6.3	13/130	2.7	0.3	2.2–3.3	8/80
Style length (cm)	7.6	1.4	4.6–9.8	13/130	3.5	0.2	2.9–3.9	8/80

four to eight for *P. pinicola*, but seeds of *P. angustifolius* consistently contained six cotyledons. Our measurements of fruits and seeds for *P. angustifolius* included ten measurements from the designated type locality in northwestern Nicaragua (Kuijt 1987) (Fig. 1, population 10). We were unable to make additional measurements of floral characters from this location because none of the many plants we observed there were flowering in March 2006.

OBSERVATIONS OF GROWTH FORM

Plant size in *P. angustifolius* varies depending on age, but we have observed plants as large as 2 m in height. Haustoria of this mistletoe can reach diameters over 15 cm and the basal diameter of stems arising from the haustorium was sometimes over 8 cm. In general, plants of *P. pinicola* are smaller than those of *P. angustifolius*. This species seldom reaches sizes larger than 1 m in height and its haustoria are usually less than 10 cm in diameter. Shoots arising from haustoria are typically less than 6 cm in diameter at their base. Plant age can be estimated by dissection of haustorial connections (Kuijt 1970) and there is a direct correlation with the age of *P. angustifolius* plants, their height, and the size of the haustorium (Howell unpublished data).

OBSERVATIONS OF PHENOLOGY AND REPRODUCTIVE BIOLOGY

In central Hondruas, *P. angustifolius* usually begins flowering in July and lasts until October. Flowering is related to elevation of the population with flowering at higher elevations starting later than at lower elevations (Martinez and Melgar 2000). Peak flowering occurs from August to September in Honduras and from June to August in Guatemala and Chiapas for *P. angustifolius*. Fruits of *P. angustifolius* are mature in March to April in central Honduras (Martinez and Melgar 2000). Flowering of *P. pinicola* begins in March and extends into December in western Belize. However, we have observed a few plants of both species flowering in March in Nicaragua and eastern Honduras. Flowers and fruits are often at different stages of development, even on the same plant, and mature flowers and fruits can frequently be found on the same *P. pinicola* plant from March to October. However, *P. pinicola*

TABLE 3. MORPHOLOGICAL CHARACTERISTICS OF THE FRUITS AND SEEDS OF *PSITTACANTHUS ANGUSTIFOLIUS* AND *P. PINICOLA*. N/n represents the number of populations sampled over the number of individual measurements.

Characters measured	*P. angustifolius*				*P. pinicola*			
	Mean	Std. Dev.	Range	N/n	Mean	Std. Dev.	Range	N/n
Fruit length (mm)	20.2	3.0	15.0–24.2	5/50	13.7	1.1	11.1–15.2	7/70
Fruit width (mm)	14.8	1.9	11.0–18.1	5/50	7.0	0.5	6.2–8.0	7/70
Seed length (mm)	15.1	1.3	12.7–17.8	5/50	12.9	0.8	10.9–14.1	7/70
Seed width (mm)	9.0	1.1	7.2–12.0	5/50	4.4	0.2	4.0–4.9	7/70

peak flowering occurs from May through October.

While these mistletoes are sympatric at several locations in Honduras and Nicaragua, we have not observed any evidence that they hybridize at these locations, even though we have observed them flowering at the same time. Although hummingbirds have been reported as key pollinators of other species of *Psittacanthus* in Mexico (Azpeitia and Lara 2006), we have only on a few occasions observed hummingbirds at *Psittacanthus angustifolius* flowers in Honduras and at *P. pinicola* flowers in Belize. Bats may be involved in the pollination of these species as well, but further research is clearly needed to confirm this hypothesis. Additional research is also needed on the animals involved in seed dispersal of these mistletoes.

Distribution of Species

Our recent studies in Nicaragua have confirmed that these mistletoes are present in the pine forests of the Cordillera Depilto and the Cordillera Jalapa near the border with Honduras. We collected *P. angustifolius* on *Pinus oocarpa*, *Pinus tecunumanii* Equiluz & J. P. Perry, and *Pinus caribaea* var. *hondurensis* (Senecl.) Barr. et Golf.; and *P. pinicola* on *Pinus caribaea* var. *hondurensis*, *P. tecunumanii*, and *P. oocarpa* (Department Nueva Segovia, Figs. 1 and 2). *Psittacanthus pinicola* has been reported to occur in the extensive *Pinus caribaea* var. *hondurensis* populations in eastern Nicaragua (Kuijt 1987; Mathiasen et al. 2003) and we examined three herbarium specimens from this region (Fig. 2, populations 17–19). We have not observed *P. pinicola* in Guatemala, but we anticipate that eventually it will be found there because it is common in the Mountain Pine Ridge region of western Belize only a few km east of Guatemala (Fig. 2, populations 2–6).

We have now collected *P. angustifolius* from nearly every Department in Honduras, and although it is widely distributed there, it is only common in Department Francisco Morazan (Fig. 1). Although we conducted additional surveys in Guatemala in March 2006, we still have only found three populations of *P. angustifolius* in central Guatemala (Department Baja Verapaz), but we expect there are many more populations in that general region, particularly in the Sierra de las Minas. Furthermore, *P. angustifolius* probably occurs in western Guatemala because it is found in Chiapas, Mexico (Fig. 1) and its pine hosts are common in western Guatemala. However, our surveys in western Guatemala have not detected it. We have observed *P. angustifolius* in El Salvador (Mathiasen et al. 2003) and we also examined a specimen of *Psittacanthus* at EAP collected from El Salvador which was labeled as *P. schiedeanus*, but the leaves and flowers of the specimen clearly indicated it was *P. angustifolius*. Therefore, we have included a second location for this taxon in north-central El Salvador in Fig. 1 (population 9). Our surveys in Chiapas, Mexico, in September 2006, also failed to uncover additional populations of *P. angustifolius* in the pine forests there. This mistletoe mainly occurs in north-central Chiapas near the villages of Jitotol and Pueblo Nuevo, but we have found one population of it near the village of Ocosingo several kilometers southeast of Jitotol (Fig. 1, population 4). It has also been reported in southwestern Chiapas, but we have not observed it there (Kuijt unpublished). Thus far, we have not observed *P. angustifolius* in Belize, but our surveys there have mainly been in the Mountain Pine Ridge region and not in the extensive *Pinus caribaea* var. *hondurensis* populations at lower elevations near the coast. It is probable that once these coastal pine forests are surveyed more intensively, many additional populations of *P. pinicola* will be found in them, and *P. angustifolius* may be discovered there as well.

The effects these mistletoes have on their pine hosts warrants further research. We have observed many dead pines infected with *P. angustifolius* in Honduras, Guatemala, and Nicaragua, so this mistletoe is associated with premature mortality of severely infected trees. Although there have been a few studies documenting that *P. angustifolius* is associated with reduced growth of severely infected *Pinus oocarpa* in Honduras (Lezama and Melgar 1999; Howell and Mathiasen 2004; Howell et al. 2005), no studies have been conducted on the effects of *P. pinicola* on its pine hosts. However, our observations in the Mountain Pine Ridge region of Belize suggest that *P. pinicola* is also associated with premature mortality of severely infected *Pinus caribaea* var. *hondurensis*, and it probably causes growth reductions of severely infected trees as well. The effect of *P. angustifolius* on the growth of pines other than *P. oocarpa* has not been investigated. Because *Psittacanthus angustifolius* has been reported to occur on oaks (Kuijt unpublished), we have specifically searched for it on oaks in Guatemala, Honduras, Nicaragua, and Chiapas, Mexico. Thus far, we have not found it parasitizing this genus.

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COLLECTION HISTORY OF *PLATANTHERA CHORISIANA* (ORCHIDACEAE) IN WASHINGTON STATE

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ABSTRACT

Although *Platanthera chorisiana* (Orchidaceae) was reportedly collected in 1912 from Lake Serene (near Edmonds), Snohomish County, Washington State, no other information about this site or collection was known. Since this original collection, it has been collected three more times in the state. Because this State Threatened orchid has never been relocated at the Edmonds site, and because it does occur at Lake Serene, near Mount Index, Snohomish County, Washington State, I reviewed potentially relevant literature and archives starting with the collection year. I documented its collection at Lake Serene, near Mount Index. The 1912 specimen passed from Harry B. Hinman, the collector and a member of the Mountaineers, to Donovan Correll, in Texas. The orchid has persisted at Lake Serene, near Mount Index, for at least 90 yrs.

Key Words: Orchidaceae, *Platanthera chorisiana*, rare plant, Washington State.

Adelbert von Chamisso (1828) first described what is now *Platanthera chorisiana* (Cham.) Reichb. f. as *Habenaria chorisiana* from the type locality mountainous regions of Unalaska. The holotype is currently at LE (Christenson 1994); a photograph of this specimen, collected by Johann Freidrich Eschscholtz, is at NY. The species name, *chorisiana*, honors Louis Choris, a Russian painter (Correll 1950). Chamisso, Eschscholtz, and Choris served on the Russian Rurik expedition, which was searching for a Northeast Passage from Russia to Alaska through the Bering Strait (Kotzebue 1821).

Platanthera chorisiana ranges from Japan northward, through the Aleutian Islands of Alaska, east to Southeast Alaska, southward through the Queen Charlotte Islands, Vancouver Island, and into Washington State (Calder and Taylor 1968; Hultén 1968; Sheviak 2002.) Several agencies and organizations rank the species as rare (State Threatened—Washington Natural Heritage Program [1997, 2003]; Sensitive—USDA Forest Service [1999]; Vulnerable—NatureServe [2004]). It is not federally listed as threatened or endangered, nor is it proposed for such listing.

Platanthera chorisiana has been reported from several sites in Washington State (Washington Natural Heritage Program 2005). Hitchcock et al. (1969) reported that *P. chorisiana* was "collected only once from our area, in 1912, from Lake Serene (near Edmonds), Snohomish County, WA." Albert E. Grable collected *P. chorisiana* from Snohomish County, Washington, in 1980 and 1986, on the Mount Baker-Snoqualmie National Forest (Grable and Laferrière 1993). I collected this species at Lake Isabel (Mt. Baker-Snoqualmie National Forest, Skykomish RD: T28N R10E S31, NE of SW. UTM e606609, n5302843 (NAD 1927). 6 August 2002, *Tracy L. Fuentes 430* (WS, WTU)). Most of the other sites have too few individuals for collection, given the rarity of this species.

Snohomish County has two lakes called Lake Serene, one near Edmonds and the other near Mount Index (Fig. 1). Because the Lake Serene near Edmonds is much farther west than the other sites of *P. chorisiana* (Fig. 1), because *P. chorisiana* has never been relocated near Edmonds, and because *P. chorisiana* does occur at the Mount Index Lake Serene (Washington Natural Heritage Program 2005), I investigated the source of the original citation in Hitchcock et al. (1969).

METHODS

I reviewed potentially relevant literature and archives dated 1912 or later to search for the Lake Serene collection. To generate farther leads, I entered the names of all paper authors and potential collectors into a search engine (http://www.google.com). To see if the specimen still existed and to document any other locality information, I contacted Pacific Northwest herbaria (ORE, OSC, WS, WSP, WTU, WWB) and then other herbaria in the United States that might possess the specimen (AMES, BRIT, GH, JEPS, LL, MO, NY, TEX, US).

RESULTS AND DISCUSSION

J. W. Thompson did not report *P. chorisiana* in his regional checklists of vascular plant species

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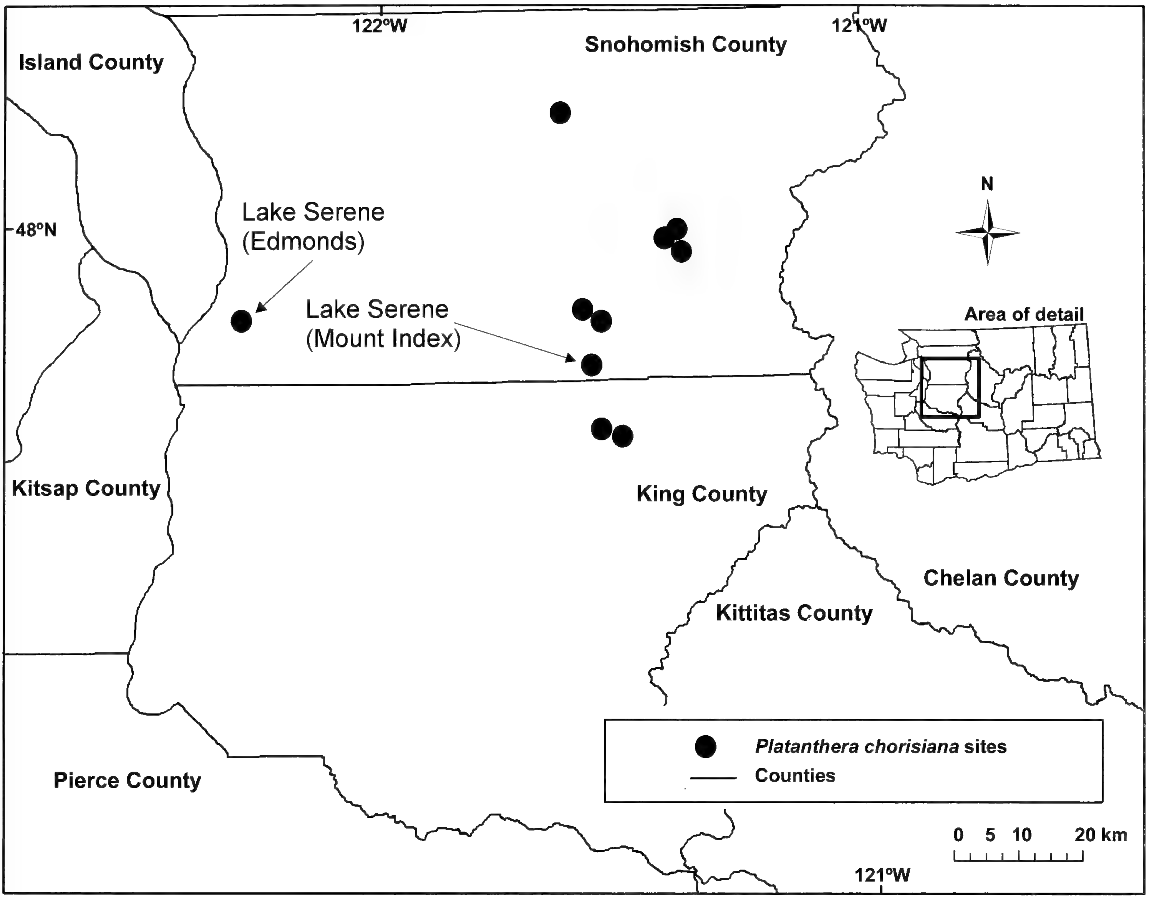

FIG. 1. Sites of *Platanthera chorisiana* in Washington State, as documented by the Washington Natural Heritage Program (2005). Two lakes in Snohomish County are named Lake Serene and reportedly had *P. chorisiana* sites. However, documentation of the westernmost site is based on Hitchcock et al. (1969) erroneously reporting that a 1912 specimen of *P. chorisiana* was collected at the Lake Serene, near Edmonds, rather than the Lake Serene near Mount Index.

(unpublished volumes, dated 1930, 1932, 1938, available at WTU).

Correll (1958) reported that he reviewed the newly acquired Oakes Ames general herbarium, consisting of about 8,000 specimens given to the Texas Research Foundation. He found a folder containing a specimen with the genus name "*Habenaria* (*Piperia*)" entered on the sheet. A note by Ames on the folder stated, "from C. V. Piper for determination." The collection date was 14 July 1912, and the locality was Lake Serene, Washington. H. B. Hinman collected the specimen.

Correll identified the specimen as *Habenaria chorisiana*, now *P. chorisiana*, and reported a new record for the United States. He noted that he contacted C. L. Hitchcock and "his observant secretary" (J. W. Thompson?) who located Lake Serene for him. They probably reviewed maps and decided that no one would be at the more remote Lake Serene by Mount Index in 1912.

However, Hinman had already climbed Mount Index in 1911 (Beckey 1987). "Mount Index lacked a documented history until October 29, 1911, when H. B. Hinman, Ernest Martin, Lee Pickett, and George E. Wright, ascending from Anderson Creek, found a flagpole on the summit." Dr. Harry B. Hinman was an active member of the Mountaineers; Mount Hinman in Snohomish County is named after him (Beckey 1987). Smith and Bailey (1910) described his keen eye for botanical oddities and his uncanny ability to reach inaccessible specimens:

> "The botany bunch was reinforced this year by a goodly company of helpers. Chief among these was Dr. H. B. Hinman, of Everett, who made practically all of the valuable collections of the trip. He would find the choicest specimens in an apparently barren spot where most of the party would declare nothing grew. He would climb perpendicular cliffs, and, clinging

to a ledge in mid-air, gather the treasures hidden from others' eyes, and all so fast that the old guard couldn't get specimens in press as fast as he brought them in."

Although I found no notes regarding a 1912 outing to Lake Serene or Mount Index, I did locate letters regarding Mountaineer plant collections. Piper and Anonymous (1913) discussed plants sent by Winona Bailey, a member of the Mountaineers, to Charles V. Piper. In a letter to Bailey, dated December 26, 1912, Piper noted, "One of the unnumbered sheets is a *Habenaria* which may be a new species. At any rate it does not look familiar, and I am going to study it more carefully." From an anonymous individual detailing more locality information, "Of the number (of plant specimens) retained by Mr. Piper, *Artemisia longepedunculata* was collected at Lake Serene on Mt. Index and has been reported but once before; the *Habenaria* is also from Lake Serene; the *Veronica* from Lake Washington."

Therefore, the 1912 specimen was collected at the Lake Serene near Mount Index, not Edmonds, passing from Harry B. Hinman, to Winona Bailey, to Charles V. Piper, to Oakes Ames, and to Donovan Correll. This specimen currently exists at LL and is in reportedly good condition (Tom Wendt, University of Texas at Austin, personal communication).

Elroy Burnett found 6 stems of *P. chorisiana* at Lake Serene, near Mount Index, on 28 July 1988 (Washington Natural Heritage Program 2005). I re-visited this site on 28 August 2002 with Laura Potash (USDA Forest Service). We found 14 stems within our monitoring plot. Thus, *Platanthera chorisiana* has persisted at Lake Serene, near Mount Index, for at least 90 yrs.

Acknowledgments

I thank Clayton Antieau, who urged me to track down the original specimen. I appreciate the help of David Giblin, Joshua Brokaw, David Morgan, Kenton Chambers, James Solomon, Emily Wood, Deborah Bell, Walter Kittredge, Rusty Russell, Thomas Zanoni, Kim Kersh, Tom Wendt, and Amanda Neill, who searched their respective collections for and me and gave me search suggestions. I thank John W. Thompson, Winona Bailey, and the Mountaineers for keeping such meticulous records. Finally, I salute Dr. Harry B. Hinman, whose sharp eye and mountaineering skills enabled the discovery of *Platanthera chorisiana* in Washington State and on the Mt. Baker-Snoqualmie National Forest.

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AN APTIAN CYCADEOID FROM THE BUDDEN CANYON FORMATION, ONO QUADRANGLE, CALIFORNIA

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ABSTRACT

We describe a cycadeoid trunk from the Aptian Chickabally Member, Budden Canyon Formation in Ono, California. Our diagnosis of the specimen as a cycadeoid was initially based on the presence of mucilage canals in the pith and the structure of the secondary xylem. This determination was subsequently supported by recognition of the distinctive morphology of the surface of the primary body of eroded cycadeoid trunks. The latter may aid in the identification of otherwise enigmatic Mesozoic fossils. This specimen is the third cycadeoid to be reported from northern California and slightly extends the known geographic range of the group within the state.

Key Words: Aptian, California, Cretaceous, cycadeoid, gymnosperm, trunk.

The cycadeoids (Bennettitales) are an extinct group of seed plants that evolved during the Triassic (248–206 Ma [mega annums]) following the formation of the supercontinent Pangea and the emergence of other seed plant groups, such as Cycadales, Ginkoales, and Glossopteridaceae (Willis and McElwain 2002). They became extinct by the end of the Cretaceous (~65 Ma). Cycadeoids attained a cosmopolitan distribution in the Mesozoic; growing abundantly in tropical and, to a lesser extent, warm temperate climates (Taylor and Taylor 1993; Willis and McElwain 2002). As a group, cycadeoids appear to have grown in disturbed habitats, particularly on levees (Retallack and Dilcher 1981). Their seeds were small and wind dispersed, commensurate with an early successional status (Tiffney 1986). Cycadeoids ranged in habit from low barrel-shaped or multi-branched shrubs to erect, often thick, sparsely branched trees. Most bore pinnately compound, coriaceous foliage (Tidwell 1998); the petioles were surrounded by lignitic scales at their point of insertion on the trunk; these scales formed the exterior surface of the trunk. Internally, the trunk consisted of a large central pith, limited primary xylem, prominent to poorly developed secondary xylem, and a thick cortical area. The secondary xylem was manoxylic, with files of tracheids separated by medullary rays that were one to three cells wide (Stewart and Rothwell 1993). Leaf traces arose from the primary xylem and passed through the secondary xylem into the cortex and directly out to the leaves. Cycadeoids were generally differentiated from the distantly related Cycads based on their vascular, reproductive, and stomatal structures (Nishida 1994). Cycadeoid stems generally lacked girdling leaf traces, which are a characteristic feature of most cycads, although they are lacking in the cycad *Antarcticycas* (Smoot et al. 1985). In addition, cycadeoids commonly had bisporangiate reproductive structures (although those of *Williamsonia* were monosporangiate) with microsporophylls and ovules within the same cone (e.g., Delevoryas 1968; Crepet 1974). By contrast, most cycads are dioecious (Stewart and Rothwell 1993).

Cladistic analyses have placed the Paleozoic medullosans as a possible ancestor to cycadeoids, based on similarities in wood structure and vascular bundle patterns (Nishida 1994; Willis and McElwain 2002). Earlier cladistic analyses suggested that cycadeoids are most closely related to angiosperms and Gnetales (Doyle et al. 1994; Nixon et al. 1994). More recent studies (e.g., Doyle 2006) generally link Gnetales with conifers (but see Hilton and Bateman 2006), while retaining a cycadeoid–angiosperm link. While some studies place cycadeoids as the sister group to angiosperms, reflecting their bisexual, flower-like reproductive structure, the lack of morphological intermediates and the presence of one, rather than two integuments, suggest some distance between the two groups (Willis and McElwain 2002).

While the group embraced a range of morphologies throughout its history, the dominant western North American Cretaceous taxon was *Cycadeoidea*, a genus of squat, barrel-trunked plants (Ward 1900; Wieland 1906–1916; Delevoryas 1968; Rothwell and Stockey 2002); although some specimens originally attributed to *Cycadeoidea* have been segregated into a separate genus, *Monanthesia* (Delevoryas 1959), and other

genera of cycadeoids were present (e.g., Stockey and Rothwell 2003). Cycadeoid fossils from California are exceedingly rare; to date, only two specimens have been reported. Ward et al. (1905) described *Cycadeoidea stantoni* from Colusa County in northern California. Delevoryas (1959) later transferred this specimen to *Monanthesia* based on vascular patterns. In 1998, an amateur fossil collector uncovered a second *Monanthesia* from Vallejo in northern California (Collecting fossils in California 1998). In this paper, we describe a cycadeoid recently collected from Aptian age sediments of northern California. This find extends the geographic range of cycadeoids within California. The specimen also has an unusual mode of preservation, which led its initial discoverer to ally it with arborescent lycopods.

FIG. 1. This portion of a Cycadeoid stem was uncovered in Cottonwood Creek, near Ono, California. The stem has been strongly eroded so that the majority of preserved tissue is pith. Leaf scars occur in a spiral arrangement, about 50° off the vertical axis.

Locality Description

The specimen was collected by Charles Dailey from Cottonwood Creek, in the Chickabally Member of the Budden Canyon Formation near Ono, California (Sec. 18, T30N, R6W). It was found on the surface, and is presumed to be derived from the immediately surrounding sediments. The Chickabally Member was determined to be of Aptian age (~120 to 112 Ma) by Murphy and colleagues (Murphy et al. 1969; Murphy 1975), who provide a detailed description of the local geology. The upper Chickabally Member is characterized by mudstone with a few sandstone beds and limestone concretions (Murphy et al. 1969).

Marine invertebrate fossils associated with this member include *Potamides diadema*, *Plicatula variata*, *Nucula gabbi*, *Turbo festivus*, and *Tessarolax bicarinata*, all suggestive of a near shore marine environment. Chandler and Axelrod (1961) described the following plant taxa as occurring in the Chickabally member, basing their identifications upon Fontaine (in Ward et al. 1905): *Cladophlebis*, *Ctenopteris*, *Sagenopteris*, *Dioonites*, *Ctenophyllum*, *Cephalotaxopsis*, *Sphenolepidium*, and *Acaciaephyllum*. These attributions are a century old, and have not been reverified for accuracy of identification or systematic assignment. However, at face value, these comprise three taxa of cycadophyte foliage, two of conifer foliage, and a single angiosperm leaf (Tidwell 1998). Chandler and Axelrod (1961) also described a putative angiosperm fruit from a nearby locality (Sec. 17, T30N, R7W). More recently, new specimens of an osmundaceous fern (Stockey and Smith 2000), a cyatheaceous tree fern (Lanz, Rothwell and Stockey 1999), and a cone of the Pinaceae (Smith and Stockey 2001) have been collected from the same general area.

General Description

The specimen is a portion of a laterally compressed, silicified, stem that is 4.5 to 5.3 cm long and 4.8 × 3.2 cm in cross section. The specimen is strongly eroded and is primarily composed of pith tissue (Fig. 1), with small, scattered portions of primary and secondary xylem located on one side. This same side of the fossil is covered with spirally arranged leaf scars. The specimen is assigned number TLLE 65 in the Collection of the Natural History Museum, Sierra College.

Pith

The pith was originally about 3.4 cm in diam. and is poorly preserved in some areas due to cell degradation (Fig. 2). Intruding sediments have occasionally permeated to the center of the fossil, and in one instance, contained a fungal spore. The majority of the preserved portion of the pith consists of thin-walled parenchyma. These cells are roughly equidimensional, averaging 110 × 105 μm in cross section and 116 × 98 μm in long section. Scattered throughout the pith are mucilage canals lined by small epithelial cells (109 × 105 μm) and bearing dark resin within. Overall, these canals are larger in diameter than the parenchyma cells, averaging 248 × 239 μm in cross section and 405 × 205 μm in long section (Fig. 3).

FIG. 2. Cross-section of specimen. Primary and secondary xylem occur in the lower left section of the specimen, below the intruded sediment.

Xylem

An approximately 5 mm wide by 1 mm thick area of primary and secondary xylem adheres to one side of the pith. A roughly 200 μm wide zone of poorly preserved cells that are interior to the secondary xylem and distinct in morphology from the pith cells is inferred to represent the place of the primary xylem. Exterior to this are radially oriented strands of alternating secondary xylem and parenchyma. Each xylem band is one to three cells wide, and is composed of dark, lignified cells averaging 28 × 25 μm in cross section. The largest band of secondary xylem (Fig. 4) is 666 μm thick. In between these bands of lignified cells are thin-walled medullary rays. Each ray is one to two cells wide, and is composed of thin-walled parenchyma cells averaging 49.6 × 40.7 μm in cross section. The limited amount of secondary xylem did not permit serial sections or a section in the tangential or radial plane.

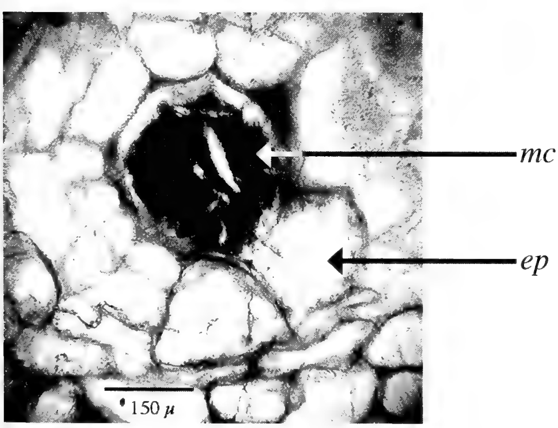

FIG. 3. Cross-section of mucilage canal (*mc*) surrounded by epithelial cells (*ep*). Note the dark contents in the interior of the canal.

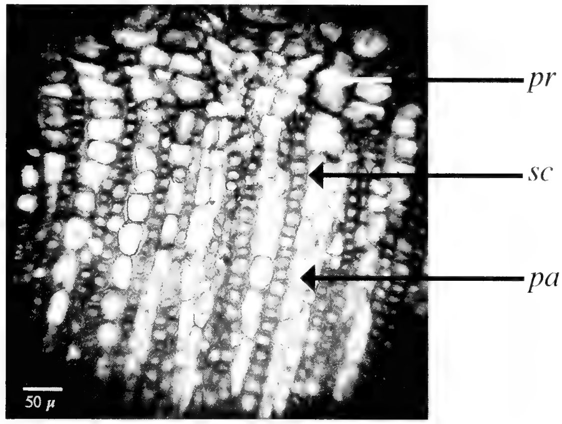

FIG. 4. Cross-section of secondary xylem. Strands of thick walled secondary xylem (*sc*) alternate with strands of parenchyma (*pa*). The interface with the primary body (*pr*) is at the top of the picture.

Leaf Scars

Spiral leaf scars occur on the same side of the specimen as the adherent secondary xylem. Five vertical spirals are present, each with four scars per spiral; the spirals incline at an angle of 49–50° off the vertical axis. Each scar ranges from 10 to 15 mm in length and 2.0 to 3.0 mm in width; a horizontal distance of 5 mm separates the scars. Leaf scars are most prominent in the center of the specimen, fading to either side.

DISCUSSION

This specimen was first presented to us as a possible Mesozoic arborescent lycopod, and indeed the spiral traces show a strong similarity to the traces observed on decorticated specimens of *Lepidodendron*. The structure of the pith, however, argued against this interpretation. Partially decorticated *Cycadeoidea* specimens from the Cretaceous of Maryland illustrated in Plate LXXXIX, Figure 2 of Ward et al.'s (1905) Later Mesozoic Floras of North America provide a view of the surface of the primary body, and exhibit a distinctive set of spiraled leaf scars, very much like those on the surface of this fossil. This led us to interpret the specimen as a cycadeoid, a conclusion further supported by the structure of the pith with its slightly elongate mucilaginous canals, and the manoxylic structure of the small amount of secondary xylem preserved.

To date, anatomically preserved cycadeoid trunks have generally been recognized by the structure of their secondary xylem and the direct path of the leaf trace, together with their reproductive organs, if present. Those with external morphology are identified by the distinctive arrangement of the surficial ramental scales and interspersed holes demarcating the

insertion of petioles. Recognition of the distinctive morphology of the exposed surface of the primary body in the Maryland specimens provides another potentially useful character, and one which allows us to ally this otherwise perplexing specimen with the cycadeoids. Recognition of this pattern of leaf traces on the surface of the primary body may aid in the identification of other anomalous Mesozoic stems, and suggests the need to examine previously described Mesozoic lycopsid axes.

Cycadeoid specimens from California are notably scarce. The present specimen is the third known. The first *Monanthesia* species was discovered in 1905 and ninety-four years passed before the second specimen of the same genus was uncovered 170 km south of the first locality. While the present specimen cannot be assigned to a specific genus of cycadeoids, its occurrence extends the range of the Californian cycadeoids by an additional 170 km to the north of the original find. These discoveries suggest that more focused research in this area would be productive.

Acknowledgments

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A NEW SUBSPECIES AND NEW COMBINATION IN *FRANGULA PURSHIANA* (RHAMNACEAE) FROM THE SIERRA NEVADA, PLUMAS COUNTY, CALIFORNIA

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ABSTRACT

We describe **Frangula purshiana** (DC.) Cooper subsp. **ultramafica** J. O. Sawyer & S. W. Edwards, an endemic to the Sierra Nevada in Plumas National Forest, and compare it with other subspecies of *F. purshiana*. We discuss the use of the generic names **Frangula** and **Rhamnus** in the California flora. We also make a new combination **Frangula purshiana** (DC.) Cooper subsp. **annonifolia** (Greene) J. O. Sawyer & S. W. Edwards.

Key Words: *Frangula*, Plumas County, *Rhamnus*, Rhamnaceae, serpentine.

Frangula purshiana (DC.) Cooper subsp. **ultramafica** J. O. Sawyer & S.W. Edwards, subsp. nov. (Fig. 1).

Frutex plerumque minor quam 2 m altus; rami alterni flexiles sine squamis hibernaculorum, cortice cinerea; ramuli virides vel cinerei vel obscure brunnei, profuse pubescentes; folia decidua vel semidecidua, prope gemmas terminales congesta; petiolus 5–15 mm longus; lamina coriacea, 50–100 mm longa, late oblonga vel ovalis vel obovata, basi obtusa vel decrescenti, apice late oblongo saepe emarginato, margine integro vel parum serrulato et plerumque undulato, pagina superiore in vivo glaucescenti vel glauca ob ceram ex caeruleo vel viridi cineream, papillata, sparse vel manifeste pubescenti vel velutina, pagina inferiore pallide viridi venis prominentibus, venis 1° et 2° valde, 3° modice pubescentibus; inflorescentia umbella axillaris; flos bisexualis; fructus putaminibus 3, in maturitate niger.

Shrub generally less than 2 m; *branches* alternate, flexible, terminal bud scales lacking; bark ash gray; twigs green to ash gray or dull brown, profusely pubescent; *leaves* deciduous or semi-deciduous, clustered near terminal buds; petiole 5–15 mm; blade coriaceous, 50–100 mm, broadly oblong, oval to obovate; base obtuse or tapered; tip broadly oblong, often emarginate; margin entire to slightly serrulate and commonly wavy; adaxial surface, when fresh, glaucescent to glaucous from a bluish or greenish gray wax, papillate, and sparsely to markedly pubescent or velvety; abaxial surface light pale green with prominent veins, 1° and 2° veins very pubescent, 3° veins moderately so; inflorescence an axillary umbel; *flower* bisexual; *fruit* 3-stoned, black at maturity.

Type: USA, CA, Plumas County, T 25N R7W sect. 11. Lat. N 40.04343 Long. W 121.15971. Elev. 1572 m. Plumas National Forest. W of Forest Service Road 26N22F ca.0.6 km (1 mile) SW from the intersection of 26N22F and 26N22 at Deadwood Saddle east of Red Hill. Hillside of serpentinized peridotite in open, mixed forest. 2 August 2004. *J. P. Smith & J. O. Sawyer 11,990* (HOLOTYPE: HSC; Isotypes: CAS, JEPS, MO, RSA)

Paratypes: USA, CA, Plumas County, Plumas National Forest. T 26N R7W sect. 33. Lat. N 40.05929 Long. W 121.20166. Elev. 823 m. ca. 4.8 km S of Caribou along the Caribou Road (Forest Service Road 27N26). Serpentine seep. 12 September 2004. *J. P. Smith & J. O. Sawyer 12,044* (HSC); T 24N R8W sect. 4. Long. N 39.912 Lat. W 121.09165. Elev. 1402 m (4600 ft). ca. 6.4 N of Spanish Ranch near Bean Hill off Forest Service Road 25N17. Douglas-fir–ponderosa pine forest. 13 September 2004. *J. P. Smith & J. O. Sawyer 12,055* (HSC); T 23N R6W sect. 21. Lat. N 39.83402 Long. W 121.30822. Elev. 1572 m (5400 ft). Duplicates to be distributed.

Miller described *Frangula* in 1754, and early botanists of the California flora used both *Frangula* (Gray 1849) and *Rhamnus* (Brewer and Watson 1880). Weberbauer (1895) considered *Frangula* a subgenus of *Rhamnus*. Wolf (1938) in his classic treatment of *Rhamnus* in North America recognized two species in California in the subgenus *Eurhamnus*—*R. alnifolia* and *R. crocea*, and three species in the subgenus *Frangula*—*R. californica*, *R. rubra*, and *R. purshiana*, based on the presence or lack of winter bud scales, thorns, type of inflorescence, sexuality, number of petals, and style length

FIG. 1. Photograph of *Frangula purshiana* subsp. *ultramafica* at the Red Hill occurrence by J. Sawyer.

differences. Bolmgren and Oxelman (2004) investigated the generic limits of *Rhamnus* using nuclear and chloroplast DNA sequence techniques. Their results showed species assigned to subgenus *Frangula* to be monophyletic and distinct from the rest of *Rhamnus*. The treatment in the forthcoming revision of *The Jepson Manual* (Sawyer 1993) will accept *Frangula* and *Rhamnus* (J. Sawyer personal communication).

Frangula purshiana subsp. *ultramafica* (Fig. 1) appears to be restricted to the Feather River complex (Alexander et al. 2007) of serpentinized peridotite and associated mafic and ultramafic substrates near Bucks Lake. The largest occurrence is on the North Fork of the Feather River near Red Hill north of Serpentine Canyon and State Route 70. The road to the top of Red Hill (1935 m) passes through open, mixed forests of *Abies concolor* (Gordon & Glend.) Lindley, *A. magnifica* A. Murray bis, *Calocedrus decurrens* (Torrey) Florin, *Pinus jeffreyi* Grev. & Balf., *P. lambertiana* Douglas, *Quercus chrysolepis* Liebm., and *Pseudotsuga menziesii* (Mirbel) Franco. Shrubs scattered with the new coffee berry include *Arctostaphylos nevadensis* A. Gray, *A. patula* E. Greene, an unusual form of *Ceanothus cuneatus* (Hook.) Nutt. (Edwards 1990; Fross and Wilken 2006), and *Quercus vacciniifolia* Kellogg. Coffee berry plants become more common at higher elevations. Other habitats include seeps, rocky streambeds; open *Pseudotsuga menziesii–Pinus ponderosa* forests and *Arctostaphylos patula* chaparral. We recommend the name "ultramafica," since plants grow on ultramafic substrates, and "Caribou coffee berry," since it grows near the mining town of Caribou.

Over a decade ago, Edwards (1990) first discussed this plant from the Red Hill area, and compared it with other *Frangula* that grow in the northern Sierra Nevada. Its firm, bluish or greenish-grayish leaves are suggestive of evergreen *Frangula californica* (Eschsch.) A. Gray subsp. *tomentella* (Benth.) Kartesz & Gandhi, but they are broader and larger. Its leaves are deciduous as in *Frangula rubra* (E. Greene) V. Grub., but it is most like *F. purshiana* (DC.) Cooper with large, broad leaves and fruits with three stones.

Another subspecies occurring in the northern Sierra Nevada is **Frangula purshiana** (DC.) Cooper subsp. **annonifolia** (E. Greene) J. O. Sawyer & S. W. Edwards comb. nov. Based on *Rhamnus anonaefolia* E. Greene, Pittonia 3: 16. 1896. Mountains of Placer County, California,

where it was collected by A. M. Carpenter in 1892. Synonymy: *Rhamnus purshiana* DC. var. *anonaefolia* (E. Greene) Jepson Man. Fl. Pl. Calif. p. 614. 1925. Greene used *Anona* P. Miller as the basis of the epithet of his new species. That name has since been replaced by *Annona* L. A second orthographic correction, based on the Article 60 of the International Code of Botanical Nomenclature (Greuter et al. 2000), recommends replacing "ae" with "i" as compounding forms, resulting in the spelling "annonifolia."

Key to Frangula purshiana taxa

1. Upper blade surface, when fresh, glaucescent to glaucous from a bluish or greenish gray wax, with papillae, and sparsely to markedly pubescent or velvety . . . . *F. purshiana* ssp. *ultramafica*

1′ Upper blade surface, when fresh, bright green, lacking a wax, papillae, and glabrous to sparsely pubescent

2. Blade base tapering; plants inland . . . . *F. purshiana* ssp. *annonifolia*

2′ Blade base rounded or heart-shaped; plants coastal. . . . .*F. purshiana* ssp. *purshsiana*

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DALEA ANALILIANA (FABACEAE: AMORPHEAE), A NEW SPECIES FROM THE NORTHWESTERN SIERRA MADRE OCCIDENTAL, MEXICO

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ABSTRACT

Dalea analiliana is described as new from the vicinity of Yécora in the Sierra Madre Occidental of eastern Sonora, Mexico. This perennial is related to *D. nelsonii* Greene, but differs in its white flowers, the presence of glands on both surfaces of the leaflets, and its more northern distribution. *Dalea analiliana* occurs in open grasslands and along roadsides in oak and oak-pine forest habitats similar to those described for *D. nelsonii*.

RESUMEN

Se describe la especie nueva **Dalea analiliana** de los alrededores de Yécora en la Sierra Madre Occidental al oriente de Sonora, México. Esta planta perenne está relacionada con *D. nelsonii*, pero se diferencia por sus flores blancas y la presencia de glándulas en ambas superficies de las hojuelas y su rango geográfico más al norte. *Dalea analiliana* occure en pastizal y a orillas de la carretera con zacates en bosques de encino y pino-encino, hábitates similares a los descritos para *D. nelsoni*.

Key Words: *Dalea*, Sierra Madre Occidental, North American floristics, new species.

Access to the northern Sierra Madre Occidental has progressively improved as Mexico has developed good roads in the region during the past two decades. This is particularly so with the completion of Mexico Highway 16 between the cities of Chihuahua and Hermosillo in the states of Chihuahua and Sonora respectively, finally providing easy access to Yécora approximately three centuries after the founding of the village. The vegetation has been described along the elevational transect made by this highway (Búrquez et al. 1992). More recently, several floristic projects have been completed in this general region (Estrada-C. et al. 1997; Laferriére 1994; Reina-G. et al. 1999; Spellenberg et al. 1996; Van Devender et al. 2003, 2005), resulting in the discovery of nearly 30 new taxa. The areas around Basaseachic and Yécora have been particularly rich in novelties. These restricted and more or less complete floras built upon the foundations laid by the early efforts of several botanical explorers of the general region (Gentry 1942 [revisited by Martin et al. 1998]; LeSueur 1945; White 1948). Identification of species of *Dalea* in the region was facilitated by the detailed revision of that genus and allied genera by Rupert Barneby (1977).

The new *Dalea* described herein is readily assignable to the section *Thornbera* (Rydb.) Barneby by its perennial, herbaceous habit, the 10-merous androecium with epistemonous petals perched half-way between the hypanthium and anthers, and the deeply separated filaments in a tassle about as long as the sheath (Barneby 1977). This is the tenth known species in the section as it was treated by Barneby. The specific epithet honors Ana Lilia Reina-Guerrero who, as far as is known, first collected the species with her husband, Tom Van Devender, in mid-September, 1999. Ms. Reina has studied medicinal plants of the Mountain Pima Indians in the Municipio de Yécora, and is a keen student of the flora of eastern Sonora and the Arizona-Sonora border region.

Dalea analiliana Spellenb., sp. nov. TYPE: Mexico, Sonora, Municipio de Yécora, cemetery in Yécora, 28°22′30″N, 108°56′W, very common herbaceous perennial in grassland; flowers white; 17 Sep 1999 (mid-flower), *T. R. Van Devender 99-694, A. L. Reina-G.* (HOLOTYPE: MEXU; ISOTYPES: ANSM, ARIZ, CIIDIR, MEXU, NMC, NY, UC, USON). (Figs. 1, 2).

Dalea analiliana Spellenberg, sp. nov.

Plantae characteres sectionis Thornbera (Rydb.) Barneby praebentes (Barneby 1977, p. 168), ab species ceteris sectionis differt combinatione sequentie characterium. Plantae glabrae usque ad spicas. Caules subteretes leniter vel moderate verruculosi glandibus elevatis. Foliola paribus 8–13, glandulopunctatae in superficiebus ambabus, foliolum terminale par sum pari postremo insertum (trifolium formans). Tubus calycis penitus recessus post vexillum, tubus (metiens ad sinum dorsalem) 2.5 mm longus, glaber exter, interne dentes sericeo-pilosi, orificium itaque aspectu dense ciliatum, intervallis inter costas glandibus

FIG. 1. Photo of holotype specimen of *Dalea analiliana* to be deposited at MEXU, showing habit, perennial root, and multiple stems.

parvulis aurantiacis pustuliformibus in ±2 seriebus irregularibus; dentes calycis inequales, dentes dorsales anguste triangulares 0.7 mm longi, dentes laterales late triangulares 0.5 mm longi. Petala omnino alba, vexillum 6.6 mm longum, ala 4.2 mm longa, carina alis ± aequans. Fructus glabri, glandibus paucis minutis distaliter instructi.

Plants perennial, herbaceous or weakly suffrutescent, with multiple stems arising from the crown of a woody root, glabrous to the spikes; **stems** ascending, 25–50 cm long, branched in the distal half, usually yellowish green, sometimes blushed with brownish-purple, round or very slightly ridged, lightly to moderately verruculose with round orangish glands 0.1–0.2 mm diam. densest near the nodes and on the peduncles; **stipules** narrowly linear-caudate, 1.5–3.5 mm long, yellowish, reddish or brownish; **leaves** green, imparipinnate, 3–30 mm long, subsessile or petiolate to ca. 1 mm, the rachis unwinged or with very narrow, inconspicuous green margins, intrapetiolular glands usually fused to form 1 minute gland, post-petiolular glands 2, hemispheric, orange, ±0.1 mm diam.; **leaflets** (5–) 8–13 pairs, narrowly elliptic or elliptic-oblanceolate, 1.8–5.5 mm long, flat or loosely folded, more or

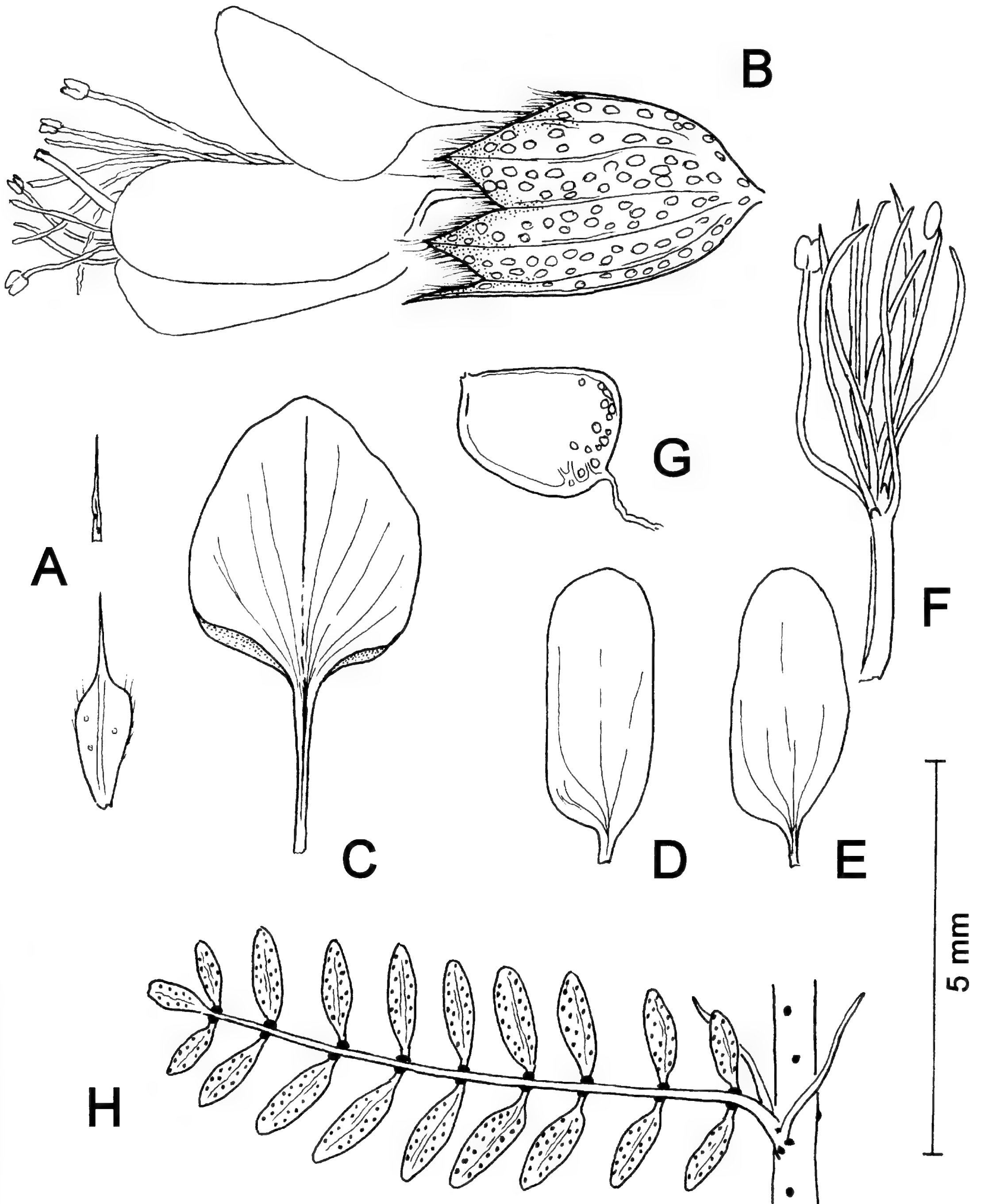

FIG. 2. Flower and leaf of *Dalea analiliana*. A. Floral bracts, range of variation; B. Flower, lateral view; C. Banner, ventral view. D. Wing petal; E. Keel petal; F. Staminal tassle, most anthers having dropped, showing epitsemonous petal-attachment scars midway on tassle; G. Fruit, lateral view, the withered style still attached; H. Leaf.

less keeled dorsally by the midrib, bluntly acute, rounded, or minutely emarginated, prominently punctuate on both surfaces with round, dark olive-green or blackish-purple glands ±0.05 mm diam., the terminal leaflet inserted at the level of the last pair and forming a trefoil; **peduncles** terminal to the main axis and all branches, 1.5–8 cm long; **spikes** dense, narrowly conic in bud and flower, ± cylindric in fruit, without petals 8–9 mm diam., the puberulent axis (1) 1.5–7 cm

long; **bracts** linear-lanceolate to narrowly lance-caudate, 3–4.5 mm, sparsely glandular, purplish-black on the caudate apical portion, the bracts in basal the portion of spike ± persistent, those distally deciduous at time of anthesis, basal bracts glabrous or glabrate on dorsal surface, minutely puberulent on ventral surface, the more distal bracts smaller and often ± puberulent dorsally; **calyx** 3.0–3.8 mm long (to the longest tooth), broadly ovoid, glabrous externally, the teeth silky-pilose within and the orifice therefore densely ciliate, the tube (as measured to a dorsal sinus) 2.2–2.5 mm long, as measured to the deeply recessed ventral sinus behind the banner ±1 mm long, purplish-black along the subfiliform ribs and on the teeth, the plane intervals between the ribs charged with 1–3 irregular rows of orange oval blister glands ±0.1 mm wide; teeth triangular or triangular-acuminate, slightly unequal, the dorsal tooth the narrowest and longest, 0.9–1.1 mm long, the lateral pair slightly shorter and proportionately broader; **petals** white (yellow according to one specimen label), eglandular, the epistemonous (attached to the androecium) ones attached just below, or the inner pair slightly above, the separation of the filaments, ca. halfway between hypanthium and anthers; banner 6.0–6.6 mm long, the claw 2.2–2.6 mm, the broadly ovate, rounded or very shallowly emarginate, slightly reflexed blade 3.8–4 mm long, 3.2–3.3 mm wide; **epistemenous petals** similar, the inner pair sometimes a little larger, the blades elliptic oblong to oblong, 3.5–3.7 mm long, 1.1–1.6 mm wide, obliquely contracted at base into a claw 0.6–1 mm long; **androecium** 10-merous, 5.8–6.8 mm long, the filament free for 3.5–4.2 mm, the connective tipped with an orange-yellow gland, the pale yellow or whitish anthers 0.4–0.8 mm long; **pod** 2.3–2.5 mm long, obliquely obovoid to obliquely trapezoidal in profile, the short style base terminal near the ventral edge, the dorsal edge and prow with a low keel, the valves hyaline except at the thinly herbaceous, sparsely gland-dotted tip.

Phenology.—Flowering in September.

Distribution and habitat.—As far as is known, *Dalea analiliana* is restricted to the Municipio de Yécora in Sonora, northwestern Mexico, with all collections from near MEX Highway 16 from 6.5 km W of Yécora to 4.8 km E of Maycoba (a linear W-E distance of ca. 37 km, approximately bounded by 28°21–24′, 108°37–58′), where it occurs in open grassy fields on consolidated mudflows and along roadsides in areas of oak and pine forest, 1500–1740 m elevation. Henrickson (1999) reviews the history of the mudflows in the area and generally describes the vegetation on these flows and the surrounding area.

Paratypes (all Sonora, Mcpio. de Yécora): Ca. 2.5 km S of Yécora, grasslands W of Arroyo El Toro, 28°20′54″N 108°56′W, 1540 m elev., occasional, flowers white; 7 Sep 1996 (early flower), *A. L. Reina-G. 96-477* et al. (ARIZ, MEXU, NY, TEX); La Otra Banda (Pima Indian portion of Yécora, open pine-oak forest on locally bar volcanic ash hilltops, 28°21′45″N, 108°55′W, 1560 m elev., uncommon herbaceous perennial, 19 Nov 1997 (fruit), *A. L. Reina-G. 97-1524* et al. (NY, WS); cemetery in Yécora, 28°22′30″N, 108°56′W, 1540 m elev., common herbaceous perennial in grassy field, flowers white, 17 Sep 1998 (early flower), *A. L. Reina-G. 98-1206*, *T. R. Van Devender* (NMC, WS); 12.4 km E of Yécora on MEX 16, pine-oak forest on steep cliff base; 28°22′50″N, 108°50′41″W, 1600 m elev., solitary herbaceous perennial on disturbed roadside, flowers white, 13 Sep 1999 (early flower), *A. L. Reina-G. 99-536*, *T. R. Van Devender* (NMC, RSA); Yécora, 28°22′25″N, 108°55′30″W, 1540 m elev., abundant herbaceous perennial on roadside, flowers white, 13 Sep 1999 (late-flower), *A. L. Reina-G. 99-547*, *T. R. Van Devender* (ARIZ, CIIDIR, MEXU, MO, NMC, US, USON); 4.8 km E of Maycoba on MEX 16, grassy valley in oak woodland, 28°24′01″N, 108°37′17″W, 1600 m elev., locally common on disturbed grassy roadside, flowers white, 15 Sep 1999 (late flower), *T. R. Van Devender 99-604*, *A. L. Reina-G.* (ARIZ, MEXU, NMC, SD, TEX,); 4.5 km W of Maycoba on MEX 16, oak woodland/grassland; 28°24′14″N, 108°41′36″W, 1500 m elev., uncommon herbaceous [perennial] on disturbed roadside; flowers white, 15 Sep 1999 (mid-flower), *T. R. Van Devender 99-609*, *A. L. Reina-G.* (ANSM, ARIZ, ASU, IBUG, NMC); 6.5 km W of Yécora on MEX 16 (km 273), pine-oak forest, 28°21′48″N, 108°58′55″W, 1740 m elev., solitary herbaceous perennial on roadside; flowers yellow, 17 Sep 1999 (late flower), *T. R. Van Devender 99-698*, *A. L. Reina-G.* (ARIZ, BRIT, NMC,); Yécora, near cemetery, 22°22′25″N, 108°56′W, 1540 m elev., locally common herbaceous perennial in grassy field; flowers white, 2 Oct 2000 (mid-fruit), *A. L. Reina. G. 2000-858*, *T. R. Van Devender* (ASC, ENCB, F, K, NMC,).

The correct identification and classification of *Dalea analiliana* has been in question from the time of the first collections. Rupert Barneby, in a communication to Dr. Van Devender, suggested that it might be near *D. urceolata* Greene, a polymorphic annual in the section *Dalea*, noting at that time that it was probably undescribed. Using Barneby's detailed keys (1977), I identified collections to be near *D. urceolata* (based on the deep notch on the calyx, behind the banner) in 2000, or near *D. ananassa* Barneby, in the section *Thornbera* in 1999 (based on perennation, proportions of the androecium, and glabrous foliage), all the time attempting to avoid the decision that this was, indeed, an undescribed taxon. Ultimately that position

could not be supported. The placement of the species is clearly in the section *Thornbera*. Within that section, *D. analiliana* s easily to near *D. nelsonii* (Rydb.) Barneby (*in* Barneby 1977), where one stalls on flower color (blue for *D. nelsonii* vs. white for *D. analiliana*), range (southern Chihuahua and adjacent Durango vs. eastern Sonora), the distribution of glands on the leaflets (abaxial versus both surfaces), and among other mensural details in the descriptions. The deeply cleft calyx aligns *D. analiliana* with the previously monotypic series *Nelsonianae* Barneby (which contained only *D. nelsonii*), adding a second, geographically adjacent species to the series.

Acknowledgments

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A NEW VARIETY OF *POTENTILLA GRACILIS* (ROSACEAE) AND RE-EVALUATION OF THE *POTENTILLA DRUMMONDII* COMPLEX

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ABSTRACT

Field studies and herbarium analyses of populations of *Potentilla* L. sect. *Graciles* (Rydb.) A. Nels. with atypical petiole vestiture result in the description of **Potentilla gracilis** Douglas ex Hook. var. **owyheensis** as a new variety, differing from var. *elmeri* and var. *flabelliformis* in having cottony-tomentose vestiture on the petioles instead of appressed to spreading straight hairs. The new variety grows in mid-montane meadows from the Owyhee Mountains in southwestern Idaho to the Ochoco Mountains in northeastern Oregon. It is conceivably of hybrid origin, with *Potentilla breweri* S. Watson providing the petiole vestiture that is otherwise unknown in *Potentilla* sect. *Graciles*. The study also resulted in the improved understanding of *Potentilla bruceae* Rydb. as a relatively coherent taxon centered in meadows around Lake Tahoe, California. As a result, *Potentilla bruceae*, *Potentilla drummondii* Lehm., and *Potentilla breweri* are recognized as distinct species, with *Potentilla subvillosa* Rydb. and *Potentilla anomalofolia* M. Peck as synonyms of *Potentilla bruceae*. *Potentilla versicolor* Rydb. is also recognized as a distinct species related to *P. breweri* but differing in having straight silky hairs rather than cottony tomentum.

Key Words: Owyhee, *Potentilla breweri*, *Potentilla bruceae*, *Potentilla drummondii*, *Potentilla gracilis*, *Potentilla versicolor*, Steens Mountain.

The *Potentilla gracilis* Douglas ex Hook. complex is the main component of *Potentilla* L. sect. *Graciles* (Rydb.) A. Nelson (Rosaceae), a section restricted to western North America. Species in the section have erect to ascending flowering stems that arise laterally to clusters of palmate (rarely subpalmate to subpinnate) leaves that are persistent at anthesis. The inflorescence is an open, many-flowered cyme in which the pedicels remain straight rather than becoming recurved in fruit. Flowers open widely at anthesis, with relatively large, yellow, obcordate petals, relatively long slender styles, and numerous smooth achenes. The *P. gracilis* complex was included in the original biosystematic investigations by Clausen, Keck, and Hiesey (1940a), who determined that the chromosomal situation was characteristic of apomictic species, comparable to that in several European *Potentilla* species complexes, with high seed set in spite of highly irregular meiosis. They also took the "almost bewildering shuffling" of morphological characters in most populations as evidence that some level of sexual reproduction was nevertheless occurring, often giving rise to well-defined ecotypes.

To reflect this complexity in a taxonomic framework, Keck (*in* Clausen et al. 1940a) chose to recognize six species in the complex: *Potentilla brunnescens* Rydb., *P. diversifolia* Lehm., *P. flabelliformis* Lehm., *P. gracilis* containing subsp. *gracilis* and subsp. *nuttallii* (Lehm.) D. D. Keck, *P. pectinisecta* Rydb., and *P. pulcherrima* Lehm. This was a significant paring-down from Rydberg's 1908 treatment of *Potentilla* for *North American Flora*, in which over 40 species in the complex (*sensu* Clausen et al. 1940a) were distributed among eight of Rydberg's "groups," intermixed with multiple other species. Peck nevertheless continued to use Rydberg's species in his *Manual of the Higher Plants of Oregon*, recognizing a dozen separate species in the first edition (Peck 1941) and several fewer in the second edition (Peck 1961). In contrast, Hitchcock et al. (1961) went one step beyond Keck and included all but *P. diversifolia* in a highly polymorphic *P. gracilis*, in which they recognized seven varieties: var. *brunnescens* (Rydb.) C. L. Hitchc., var. *flabelliformis* (Lehm.) Nutt. ex Torr. & A. Gray, var. *elmeri* (Rydb.) Jeps. (equivalent to *P. pectinisecta*), var. *pulcherrima* (Lehm.) Fernald, var. *permollis* (Rydb.) C. L. Hitchc., var. *gracilis*, and var. *glabrata* (Lehm.) C. L. Hitchc. This varietal approach has been used in other recent floras in the western United States (e.g., Ertter 1993; Holmgren 1997; Mansfield 2000), with var. *fastigiata* (Nutt.) S. Watson replacing var. *glabrata*. The *Potentilla gracilis* complex is currently being re-evaluated as part of the upcoming treatment of *Potentilla* in volume 9 of *Flora of North America North of Mexico*,

which will include keys to and descriptions of all taxa. Optimum circumscriptions have not yet been finalized, and will remain provisional due to the biological complexities noted by Clausen et al. (1940a).

The present paper focuses on a series of anomalous populations in *Potentilla* sect. *Graciles* that have cottony to shaggy pubescence on the petioles, in contrast to the straight appressed to spreading petiole hairs that otherwise characterize the section. This focus was triggered by multiple collections from the Mud Flat area of Owyhee County, Idaho, that have a distinct cottony-tomentose vestiture on the petioles. Field work in 2006 confirmed that plants with this vestiture type form relatively uniform populations in the Owyhee Uplands of southwestern Idaho. These plants are distinctive enough in other regards (e.g., adaxially silver-gray leaflets that are often secondarily lobed) to stand out when growing in mixed populations with other members of the *P. gracilis* complex, as is routinely the case. Further examination of specimens in herbaria in Idaho and Oregon shows that the taxon also occurs in higher elevations of southeastern Oregon and is widespread in the Ochoco Mountains, primarily in scattered "prairies" surrounded by mixed conifer forest.

Before describing the "Mud Flat" entity as a new taxon, it was first necessary to determine its relation to several of Rydberg's many species names currently residing in synonymy, most of which were based only on type specimens. Of particular significance is *Potentilla subvillosa* Rydb. (page 316 in Rydberg 1908), based on *Hansen 297* collected in 1892 from Carson Spur in Alpine County, California. Keck (*in* Clausen et al. 1940a) considered this collection comparable to *P. pectinisecta* except for the presence of dense tomentum on the leaves and suggested that it might prove to be subspecifically distinct. Petiole vestiture on *Hansen 297* does in fact overlap that of the "Mud Flat" entity, opening the possibility that *P. subvillosa* represents the same taxon, and accordingly an existing available name, although occurring significantly farther south with no intervening populations known. Field work at and near Carson Spur in September 2006 confirmed, however, that extant plants comparable to the type of *P. subvillosa* from the type locality differ sufficiently from the "Mud Flat" entity to be considered separate taxa; i.e., shaggier petiole vestiture and less silvery-gray leaves that are frequently subpalmate. The Carson Spur material was furthermore determined to be representative of a relatively consistent entity that is locally abundant in meadows around Lake Tahoe and that extends into southern Oregon, with taxonomic implications discussed after the following new description.

Description and Discussion of Potentilla gracilis var. owyheensis

As a result of these field and herbarium studies, the "Mud Flat" entity is described here as *Potentilla gracilis* var. *owyheensis*. For the sake of consistency with current floras, we have decided to use varietal status, with the realization that further study might indicate that the distinctiveness of var. *owyheensis*, and for that matter other varieties in *P. gracilis*, is equivalent to that which characterizes apomictic species elsewhere in *Potentilla*. In the following description, leaflet measurements are for basal leaves, and the largest floral dimensions occur on the earliest flowers of the season.

Potentilla gracilis var. **owyheensis** Ertter & D. Mansfield, var. nov. (Fig. 1)—TYPE: USA, Idaho: Owyhee Co., northeast of Nickel Creek crossing on Owyhee Uplands National Back Country Byway (Mud Flat Road) between Owyhee Mountains and Juniper Mountain, 30–40 air miles SE of Jordan Valley (Oregon), dry meadow below juniper woodland on rhyolitic substrate, 42°32.90′N 116°46.01′W, ca 5400 ft., 5 Jul 2006, *B. Ertter 18688 with D. Mansfield and E. Yensen* (Holotype UC; isotypes CIC, ID, K, MO, NY, OSC, PR, RM, WTU)

Potentilla gracilis var. *elmeri* et var. *flabelliformis* primo adspectu maxime simile, sed petiolis gossypinis nec strigosus nec hirsutus.

Tufted perennial from sturdy branched caudex. **Stems** decumbent to ascending-erect, arising laterally to leaf tufts, (15–)30–60 cm long, ± cottony-tomentose to weakly pilose. **Leaves** palmate, the primary leaves basal; petiole (3–)5–15(–19) cm long (largest on Steens Mountain), ± cottony-tomentose, sometimes weakly pilose with tangled hairs 1–1.5 mm long; leaflets 5–7, ± obovate, the central leaflet (2–)3.5–7 cm long, toothed ca. (1/2–)3/4 to midvein with 4–8 teeth per side, the teeth ± tapering from base, sometimes secondarily toothed or lobed, the underside ± cottony-tomentose on surface and strigose on veins, the upper side less densely pubescent but still grayish with a mixture of cottony and pilose hairs; cauline leaves 1–4, reduced in size. **Inflorescence** congested at early anthesis, openly branched in fruit, comprising 1/4–2/3 of stem length, (5–)10–60-flowered; pedicels ± straight, 4–12(–20) mm long, whitely pilose with a mixture of crisped and fine straight hairs <1 mm long. **Flowers:** hypanthium shallow, externally pilose with loose silky-shaggy hairs ± 1(–2) mm long; sepals 4–7 mm long, acute—acuminate, sometimes purple-tipped; epicalyx bractlets ± narrowly lanceolate-elliptic, 2–5(–6) mm long, 1/2 to nearly as long as sepals; petals broadly obovate to obcordate, ± retuse, (3–)4–

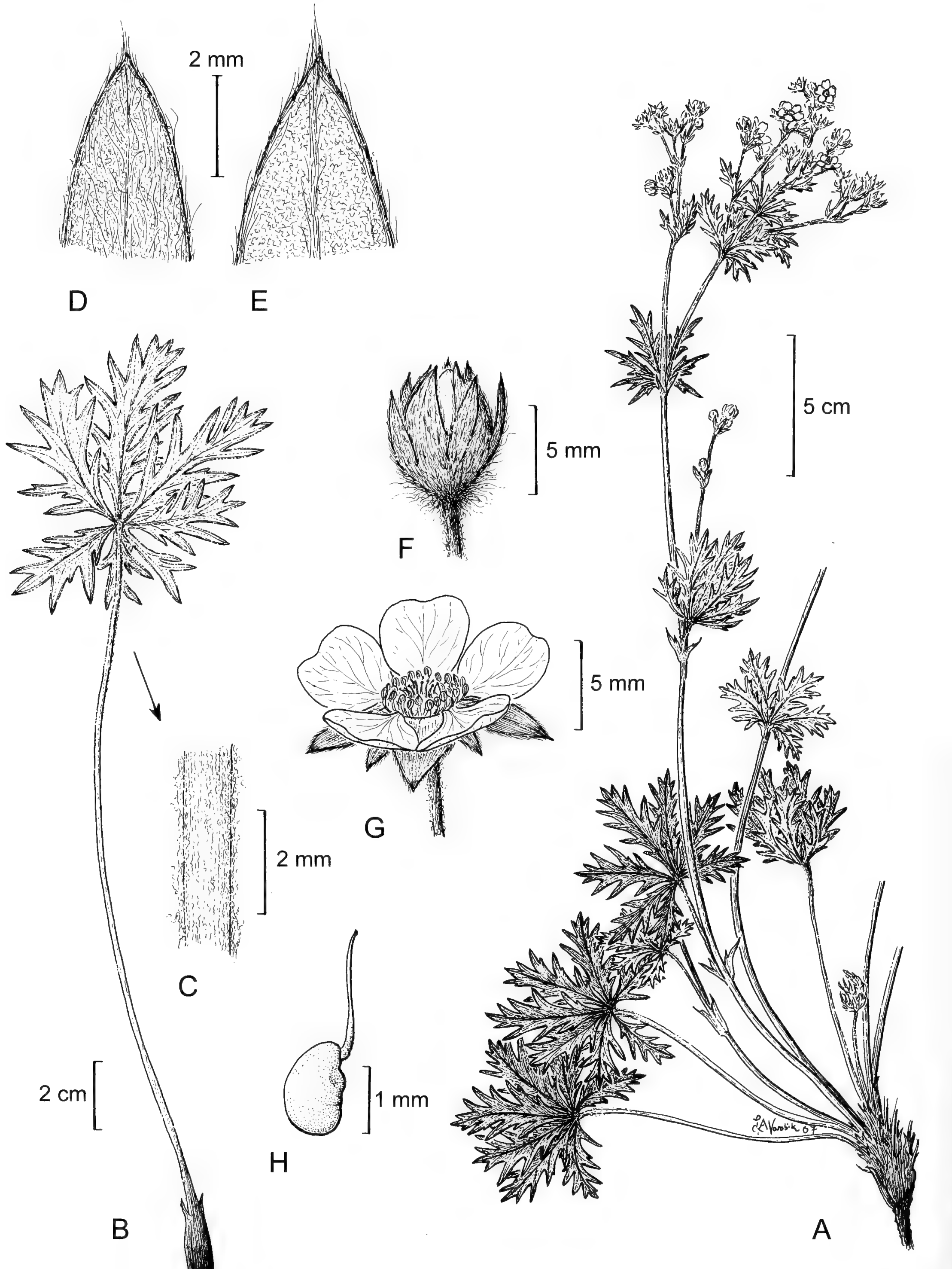

FIG. 1. *Potentilla gracilis* var. *owyheensis*. A. Habit. B. Basal leaf. C. Enlargement of cottony-tomentose vestiture on petiole. D. Vestiture on adaxial leaflet tip. E. Vestiture of abaxial leaflet tip. F. Flower bud, showing pilose vestiture. G. Opened flower. H. Achene and style. (A–G drawn from *Ertter 18680* and *18688*; H from *Ertter 18696*.)

6(–11) mm long, >sepals, bright yellow; filaments 1–3.5 mm long; anthers 0.8–1.1 mm long; styles 1.5–2.5 mm long, ± tapering from somewhat glandular-thickened base. **Achenes** ± 1.5 mm long, light brown, smooth.

Additional specimens. USA, **Idaho: Owyhee Co.**, Mud Flat, 44 mi SW of Grandview, 17 Jun 1943, *J. H. Christ 14079* (UC), Cottonwood Creek crossing on Owyhee Uplands National Back Country Byway (Mud Flat Road) between Owyhee Mts. and Juniper Mt., 5600 ft., 5 Jul 2006, *B. Ertter 18680 with D. Mansfield & E. Yensen* (CIC, UC), same location as *Mansfield 05-174*, 5 Jul 2006, *B. Ertter 18696 with D. Mansfield & E. Yensen* (CIC, UC), Pleasant Valley area ca 1½ mi. N of Mud Flat Rd., 11 Jun 1980, *D. Henderson 5567 with C. Wellner* (ID), 3 mi SW of Mud Flat on road to Juniper Mt., 7 Jun 1946, *B. Maguire & A. H. Holmgren 26306* (COLO, MO, UC, US, WTU), Mudflat Road 1.4 mi W of Juniper Mt. turnoff, 5670 ft., 9 Jun 2005, *D. Mansfield 05-174* (CIC, UC), Payne Cabin, Juniper Mt., ca 6150 ft., 14 Jul 1971, *P. L. Packard 71-257a* (CIC), along Mud Flat Road just past crossing of Battle Creek heading south, 5000 ft., 31 May 1993, *J. F. Smith 249* (SRP). **Oregon: Crook Co.**, Ochoco Forest, 22 Jun 1932, *M. E. Peck 17071* (WILLU), Summit Meadow, Ochoco Forest, 21 Jun 1932, *M. E. Peck 17078* (WILLU); **Grant Co.**, junction of State Rt. 16 and 63 in Summit Prairie, ca 5300 ft., 25 Jul 2006, *B. Ertter & J. F. Smith 18724* (SRP, UC), Logan Valley, 7 Aug 1946, *B. Maguire & A. H. Holmgren 26900* (NY, UC), moist ground 5 mi E of Austin [duplicate sheet: 5 mi E of Prairie City], 20 Jun 1938, *M. E. Peck 19899* (WILLU), Summit Prairie, 5775 ft., 11 Jul 1937, *E. H. Reid & R. Collins 554* (ORE); **Harney Co.**, Steens Mt., Fish Lake, 14 Jul 1943, *J.Davis s.n.* (WILLU), Steens Mt., S side of Fish Lake, 15 Aug 1996, *Ertter 15232* (CIC, UC), Steens Mt., south leg of Loop Road 1.2 mi from rim, ca. 8800 ft., 15 Aug 1996, *Ertter 15253* (CIC, UC), Steens Mt. 15.5 mi due ESE of Frenchglen, 7200 ft., 9 Jul 1953, *C. G. Hansen 341* (OSC), Steens Mt., meadow between Lily Lake and Fish Lake, 31 Jul 1946, *B, Maguire & A. H. Holmgren 26761* (UC, WTU), Steens Mt., flat 3/4 mi N of Fish Lake between McCoy Cr. and Big Fir Cr., 7500 ft., 21 Jun 1990, *D. Mansfield 90-286* (CIC), Steens Mt., Fish Lake/Blitzen divide across road from Lost Lake turn, 8160 ft., 23 Jul 1991, *D. Mansfield 91-367* (CIC), Bear Valley, [N of] Burns, Jun 1937, *C. C. Parsell s.n.* (OSC), meadow along Silver Creek 6 mi W of Riley, 22 Jun 1925, *M. E. Peck 13907* (WILLU), Myrtle Park, 5 Jul 1941, *M. E. Peck 21009* (WILLU), Steens Mt., open mountain meadows above Fish Lake, 8000 ft., 16 Jul 1935, *J. W. Thompson 12133* (UC, WILLU, WTU); **Malheur Co.**, reservoir ca. 5 mi E of Jackson Creek Pass in upper Antelope Creek drainage, ca. 5800 ft., 2 Jul 1999, *D. Mansfield 99-136* (CIC), 8 air mi NE of McDermitt, 6400 ft., 12 Jun 2002, *D. Mansfield 02-417 with H. Kugler, H. Nielsen, & J. Loehrke* (CIC); **Wheeler Co.**, near summit of Ochoco Pass, 1555 m, 11 Jun 1941, *L.E. Detling 4841* (ORE).

Phenology, habitat, and distribution. Flowering May to July (August). Growing in vernally moist meadows that dry out during the summer, surrounded by *Artemisia* L., *Juniperus* L., *Populus tremuloides* Michx., *Pinus ponderosa* Douglas ex C. Lawson, and/or other conifers, from 1200 to 2700 m elevation in the Owyhee uplands and Ochoco, Aldrich, and Steens mountains of southeastern Oregon and adjacent Idaho.

Potentilla gracilis var. *owyheensis* characteristically occurs in mid-montane meadows that are vernally wet but dried by mid-summer. As is commonly the case for *P. gracilis*, multiple varieties regularly occur in the same meadows, notably var. *elmeri* or var. *flabelliformis* and var. *fastigiata* s.l. In such situations, there is generally at least some level of ecological stratification and phenological separation, with var. *owyheensis* dominating the drier periphery of the meadow and tending to have an earlier blooming period. In some populations (e.g., most of those in Owyhee County), there is very little evidence of intergradation between var. *owyheensis* and co-occurring varieties of *P. gracilis*, but some other populations (e.g., *Ertter & Smith 18724*) include plants with intermediate vestiture on the petioles and leaflets.

Most historical collections of *Potentilla gracilis* var. *owyheensis* have been distributed as *P. pectinisecta* (=*P. gracilis* var. *elmeri*) and would key to either this taxon or *P. gracilis* var. *flabelliformis* in regional floras (Hitchcock et al. 1961; Hitchcock and Cronquist 1973; Holmgren 1997). Peck's collections of var. *owyheensis* were variously identified as *P. flabelliformis*, *P. blaschkeana* Turcz., or *P. permollis* Rydb. *Potentilla gracilis* var. *owyheensis* resembles var. *elmeri* and var. *flabelliformis* in having leaflets deeply divided into slender lobes, but differs from both varieties, and all other members of the *P. gracilis* complex, in having more or less cottony-tomentose pubescence on the petioles and both surfaces of the leaflets. In contrast, the other taxa only have relatively straight hairs that are spreading to appressed on the petioles, and any tomentum is absent or confined to the underside of the leaflets. As a result, var. *owyheensis* is conspicuously more silvery than co-occurring members of the *P. gracilis* complex. In addition, the leaflet teeth of var. *owyheensis* tend to be more irregular in size and shape, and are sometimes secondarily toothed or lobed.

Tentatively included in the current circumscription are specimens from near Fish Lake on

Steens Mountain that have served as the basis for the erroneous inclusion of *Potentilla quinquefolia* Rydb. in Oregon (Peck 1941, 1961; Hitchcock et al. 1961). These populations were treated by Mansfield (2000) as *P. gracilis* var. *elmeri* with introgression from *P. breweri* S. Watson, a high-montane species with abundant cottony tomentum. Unequivocal var. *owyheensis* occurs elsewhere on Steens Mountain (*Ertter 15253*), but many of the Fish Lake specimens are unusually short, with relatively short styles and intermediate vestiture. In that Steens Mountain is one of the areas where *P. breweri* is sympatric with multiple members of the *P. gracilis* complex, it is possible that these intermediate specimens do in fact result from hybridization between the two species. Indeed, introgression from *P. breweri* could underlie the origin of var. *owyheensis* itself, thereby accounting for a petiole vestiture type otherwise unknown in the *P. gracilis* complex. If so, var. *owyheensis* is now a well-established taxon, with a relatively high degree of morphological and ecological consistency throughout its range.

One additional specimen of possible relevance to *P. gracilis* var. *owyheensis* is a collection by David Douglas from "Valleys of the Blue Mountains, 1826," seen and photographed by one of us (Ertter) at K. The leaflet lobing and locality are compatible with var. *owyheensis*, such that the Douglas specimen could represent the oldest known collection of an overlooked variety, languishing among unidentified *Potentilla* for nearly 180 years. The specimen's original (mis)-identification as *Potentilla arachnoidea* (Lehm.) Douglas ex Rydb. carried a tantalizing hint of cobwebby petiole vestiture, although this name is a synonym of the unrelated *P. pensylvanica* L. However, close-up photographs made available to us, and an examination of the specimen by R. Brummitt, indicate that the petiole vestiture consists of relatively straight hairs comparable to those found in other members of the *P. gracilis* complex, not the cottony-tomentose hairs of var. *owyheensis*.

POTENTILLA SUBVILLOSA AND THE P. DRUMMONDII COMPLEX

As previously noted, the type of *Potentilla subvillosa* falls within a taxon that has some similarities to *P. gracilis* var. *owyheensis* but which has petioles with shaggier hairs and leaves that are frequently subpalmate, and which occurs well to the south of var. *owyheensis*. Field work has shown this entity to be a relatively consistent, locally abundant taxon in meadows around Lake Tahoe, characterized by irregularly subpalmate leaves and petiole vestiture ranging from villose to tomentose. Vouchers include *Ertter et al. 18770* (Carson Spur, Amador Co., CA), *Ertter et al. 18775* (Kirkwood Meadow, Amador Co., CA), and *Ertter et al. 18493* (Tahoe Meadows, Washoe Co., NV), all at UC with numerous duplicates to be distributed.

Comparable herbarium specimens occur further north in California and southern Oregon, allowing for variation in leaf dissection. This includes the type of *Potentilla bruceae* Rydb. from the Warner Mountains of Oregon, which has been treated as a subspecies or variety of *P. drummondii* Lehm. in recent floras (Ertter 1993; Holmgren 1997). The two taxa, plus *P. breweri*, comprise the *P. drummondii* complex as defined by Clausen et al. (1940b), which is closely related to the *P. gracilis* complex and shares an equally complex chromosomal situation indicating probable apomixis. In conjunction with their transplant experiments on the complex, Clausen et al. (1940b) treated *P. bruceae* as *P. drummondii* subsp. *bruceae* (Rydb.) D. D. Keck, but retained *P. breweri* as a separate albeit closely related species. They interpreted the regular occurrence of intermediates where the species occurred sympatrically, as was frequently the case, as evidence of hybridization and recombination. One of us (Ertter 1992) went one step further and treated *P. breweri* as *P. drummondii* subsp. *breweri* (S. Watson) Ertter, with the speculation that subsp. *bruceae* existed primarily as sporadic recurring hybrids between the two extremes.

As a result of the current investigation, this taxonomic stance is being reversed, with *Potentilla bruceae* being used at the species level to accommodate the relatively uniform populations noted previously, occurring in northeastern California and south-central Oregon. This circumscription includes the type of *P. subvillosa* and probably *P. anomalofolia* M. Peck, though the latter has more dissected leaves than typical *P. bruceae*. *Potentilla drummondii* in the narrow sense and *P. breweri* are also being treated as species, with *P. bruceae* and *P. drummondii* placed in *P.* sect. *Graciles*. *Potentilla breweri*, on the other hand, is provisionally placed in *P.* sect. *Multijugae* (Rydb.) A. Nelson on the basis of its pinnate leaves and more prostrate habit, although the cottony vestiture and straight pedicels are anomalous in the section. Such an arrangement can only be done with full acknowledgement that hybridization and introgression among species and across sections is routinely occurring, but this is evidently the norm for apomictic sections of *Potentilla* worldwide.

Another species closely related to *Potentilla breweri* is *P. versicolor* Rydb., which was considered a synonym of *P. breweri* by Clausen et al. (1940b), but which Hitchcock et al. (1961) treated as a synonym of *P. ovina* J. M. Macoun, and Holmgren (1997) treated as a synonym of *P. millefolia* Rydb. Plants comparable to the type of

P. versicolor are common on Steens Mountain, Oregon (Mansfield 2000), and also occur in the Wallowa Mountains of Oregon (e.g., *M. E. Peck 18484*, UC) and the Ruby Mountains in Elko County, Nevada (e.g., *N. H. Holmgren & P. K. Holmgren 10995*, UC). Such plants resemble *P. breweri* in habit and habitat but differ in having straight silky hairs rather than cottony tomentum. *Potentilla versicolor* will accordingly be recognized as a distinct species in *Flora of North America* and has already been treated as such by Mansfield (2000). The species is not currently known from California, but the type of *P. millefolia* var. *algida* Jeps. from Trinity County, California, is transitional from *P. breweri* to *P. versicolor*.

The complete synonymy for *Potentilla drummondii*, *P. bruceae*, *P. breweri*, and *P. versicolor*, as here circumscribed, is presented below. Not included is *Potentilla breweri* var. *viridis* Jeps., which is evidently a hybrid between *P. breweri* and *P. wheeleri* S. Watson, as previously discussed by Ertter (1992).

Potentilla drummondii Lehm.

Potentilla drummondii Lehm., Nov. Stirp. Pug. 2: 9. 1830. *P. dissecta* var. *drummondii* (Lehm.) Kurtz, Bot. Jarhb. Syst. 19: 374. 1894. TYPE: Canada: "in the Rocky Mountains, north of the Smoking River," *Drummond s.n.* (E! K! PR!)

Potentilla cascadensis Rydb., Mem. Dept. Bot. Columbia Coll. 2: 109. *P. drummondii* var. *cascadensis* (Rydb.) Th. Wolf, Biblioth. Bot. 16, Heft 71: 492. 1908. TYPE: USA, Washington: Skamania Co., Chiquash Mts., 14 Sep 1896, *Suksdorf 2165* (Holotype NY!; isotypes CAS! GH! MO! UC! US!)

Potentilla bruceae Rydb.

Potentilla bruceae Rydb., N. Amer. Fl. 22: 342. 1908. *P. drummondii* subsp. *bruceae* (Rydb.) D. D. Keck, Publ. Carnegie Inst. Wash. 520: 180. 1940. *P. drummondii* var. *bruceae* (Rydb.) N. H. Holmgren, Intermount. Fl. 3(A): 94. 1997. TYPE: USA, Oregon: Lake Co., Warner Mts., Jul 1898, *Mrs. C. C. Bruce 2301* (Holotype NY!; isotypes DS! fragment at UC!)

Potentilla subvillosa Rydb., N. Amer. Fl. 22: 316. 1908. TYPE: USA, California: Amador [Alpine on label] Co.: Carson Spur, 1892, *G. Hansen 297* (Holotype NY!; isotype MO!)

Potentilla anomalofolia M. Peck., Proc. Biol. Soc. Wash. 49: 110. 1936. TYPE: USA, Oregon: Klamath Co., 3 mi N of Klamath Agency, 10 Jul 1933, *M. E. Peck 16819* (Holotype WILLU in OSC!; isotypes UC! WILLU! WS!)

Potentilla breweri S. Watson

Potentilla breweri S. Watson, Proc. Amer. Acad. Arts 8: 555. 1873. *P. drummondii* subsp. *breweri* (S. Watson) Ertter, Brittonia 44: 430. 1992. *P. drummondii* var. *breweri* (S. Watson) N. H. Holmgren, Intermount. Fl. 3(A): 92. 1997. TYPE: USA, California: "summit of Mono Pass," 27 Jun 1863, *W. H. Brewer 1720* (Holotype US!; isotypes GH! JEPS! UC! YU!)

Potentilla breweri var. *expansa* S. Watson in W. H. Brewer & S. Watson, Bot. California 1: 179. 1876. TYPE: USA, California: Sierra Co., 1874, *J. G. Lemmon 64* (Holotype GH!; isotype NY!)

Potentilla plattensis Nutt. var. *leucophylla* Greene, Erythea 1: 5. 1893. TYPE: USA, California: Nevada Co., Independence Lake, 26 Jun 1892, *C. F. Sonne s.n.* (MO! NY! UC!)

Potentilla millefolia Rydb. var. *algida* Jeps., Fl. Calif. 2: 186. 1936. TYPE: USA, California: Trinity Co., North Fork Swift Creek, Salmon Mts., July 1909, *H. M. Hall 8698* (Holotype UC!)—transitional to *P. versicolor*

Potentilla versicolor Rydb.

Potentilla versicolor Rydb., N. Amer. Fl. 22: 344. 1908. TYPE: USA, Oregon: Lake Co., Gearhart ("Grayheart") Butte, 9 Aug 1896, *F. V. Coville & J. B. Leiberg 307* (Holotype US!; fragment at NY!)

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BRODIAEA SANTAROSAE (THEMIDACEAE), A NEW RARE SPECIES FROM THE SANTA ROSA BASALT AREA OF THE SANTA ANA MOUNTAINS OF SOUTHERN CALIFORNIA

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ABSTRACT

Brodiaea santarosae (Themidaceae) is a new species from southwest Riverside County and immediately-adjacent Miller Mountain of San Diego County, CA. It is easily distinguished from other *Brodiaea* species in southern California by its large flowers and distinctive, variable staminodes; morphological analysis revealed 11 total differentiating characteristics. *Brodiaea santarosae* occurs only on or very close to the 8–11 million-year-old Santa Rosa Basalt. It has the smallest range of the southern California *Brodiaeas*, with just four known populations occupying only a small portion of a ~40 km^2 area, plus a fifth small population disjunct by 11 km.

It has been speculated that the *B. santarosae* population is a hybrid swarm between *B. filifolia* and *B. orcuttii,* based solely on the appearance of the staminodes and filaments in selected flowers. This speculation was rejected due to the lack of sympatry between the three taxa and because specimens of *B. santarosae* have numerous characteristics that are not intermediate between the claimed parent taxa. In contrast, intermediate characteristics were seen in F1 specimens of *B. filifolia* X *B. orcuttii* discovered in San Marcos, CA, the only location where those species overlap.

We also report extensions to the length characteristics for both *B. filifolia* and *B. orcuttii* and demonstrate that two populations of *B. filifolia* previously thought to be hybrids are consistent with other *B. filifolia* populations.

RESUMEN

Brodiaea santarosae (Themidaceae) es una nueva especie del sudoeste del Condado de Riverside y del monte Miller inmediato-adyacente en el Condado de San Diego, CA. Es distinguido fácilmente de las otras especies de *Brodiaea* del Sur de California por sus flores grandes y staminodes variables y distintivos; el análisis morfológico reveló 11 totales que distinguen características. *Brodiaea santarosae* ocurre solamente en o muy cerca del Santa Rosa Basalt de 8–11 millones de años de antigüedad. Tiene la gama más pequeña de las *Brodiaeas* del Sur de California, con apenas cuatro poblaciones conocidas ocupando solamente una porción pequeña de un área de ~40 km^2, más una quinto población pequeña disjunta por 11 kilómetros.

Se ha especulado que la población de *B. santarosae* es un enjambre híbrido entre *B. filifolia* y *B. orcuttii*, basados solamente en el aspecto de los staminodes y de los filamentos en flores seleccionadas. Esta especulación fue rechazada debido a la carencia de sympatry entre los tres taxa y porque los especímenes de *B. santarosae* tienen características numerosas que no sean intermedias entre los taxa demandados del padre. En contraste, las características intermedias fueron consideradas en los especímenes F1 del *B. filifolia* X *B. orcuttii* descubierto en San Marcos, CA, la única localización donde esas especies se traslapan.

También divulgamos extensiones a las características de la longitud para *B. filifolia* y *B. orcuttii* y demostramos que dos poblaciones del *B. filifolia* pensaron previamente para ser híbridos son constantes con otras poblaciones del *B. filifolia*.

Key Words: Basalt, *Brodiaea*, California, endemic, Peninsular Ranges, Santa Ana Mountains, Santa Rosa Basalt, Santa Rosa Plateau.

We describe here a new species of *Brodiaea* that has previously been collected by at least six different botanists and variously determined as *B. orcuttii* (E. Greene) Baker, *B. filifolia* S. Watson, or a hybrid between the two (see paratype specimens cited below, as well as Boyd et al. 1992, 1995).

The confusion stems from the remarkable variation in the staminodes in this species. About 10% of the flowers of this species have no staminodes and long filaments, superficially resembling the flowers of *B. orcuttii.* Approximately another 5–10% have short recurved filiform staminodes and shorter filaments, superficially resembling the flowers of *B. filifolia.* The majority of the flowers have longer staminodes and variable-length filaments, which in the absence of quantitative analysis appeared to be hybrids between those taxa.

The recognition of this new species came from a research program of the first two authors on hybrids of various *Brodiaea* species in southern California, combined with the discovery by the third author of a large accessible population of this new species. Analysis of that population revealed that it was not consistent with any previously-known southern California *Brodiaea* species, nor did it seem consistent with a hybrid swarm between any of those species.

This discovery came in time to survey many of the relevant *Brodiaea* populations in Riverside and San Diego Counties during the 2006 season. During that survey, we found three specimens from San Marcos that appear to be true hybrids between *B. filifolia* and *B. orcuttii*. These specimens were valuable in confirming that this new species was not of hybrid origin.

We were able to obtain and analyze enough fresh specimens from enough populations to determine that this entity warranted recognition as a new species that is distinguished from *B. filifolia* and *B. orcuttii* by at least 11 separate characteristics. This new species has the smallest range of the southern California *Brodiaeas* and is found only on or very close to the 8–11 million-year-old Santa Rosa Basalt.

Our analysis also showed that two populations of *B. filifolia* previously thought to be hybrids are consistent with other *B. filifolia* populations. This adds two protected populations of *B. filifolia* to the list in U.S. Fish and Wildlife Service (2004). These populations were omitted from that list since hybrids are not as important as pure populations for the conservation of the species.

Species Description and Distribution

Brodiaea santarosae T. Chester, W. Armstrong & K. Madore, sp. nov. (Fig. 1)

Differt a *B. filifolia* filamenta 2.4–8.2 mm. Differt a *B. orcuttii* staminodia praesens in 90% de flores, acuminatus, 0–7 mm; perianthii tubi 6.0–11.3 mm; anthera 5.4–8.9 mm; ovaria 3.5–8.2 mm; et styli (includens stigmata) 10.5–17.0 mm.

Geophyte; glabrous; *corm* 15–25 mm high, 25–31 mm wide, producing cormlets at the sides; *leaves* 2–4, basal, linear, appearing before the inflorescence; *inflorescence* scapose, 1–2 scapes per corm, scape 8.8–36 cm, umbellate; *flowers* 2–6 in terminal umbels, erect on pedicels 18–107 mm long and 1.1–1.9 mm wide at distal end; *bracts* at base of umbel, scarious, 6.5–11 mm; *corolla* blue-purple, campanulate, base 2.0–3.9 mm wide, tube 6.0–11.3 mm, lobes 6, ascending, 15.4–29.5 mm; *ovary* green, 3.5–8.2 mm; *style* including stigma 10.5–17.0 mm, stigma 3-lobed, with one lobe usually slightly above the other two, distal end of stigma from 3.0 mm below to 1.4 mm above distal end of anthers; *anthers* barely exserted from corolla tube, filaments 2.4–8.2 mm, anther sacs 5.4–8.9 mm; *staminode* present in 90% of flowers, white to lavender, tapered to tip, free portion 0.0–7.0 mm, usually variable in length within individual flowers; *fruit* loculicidal capsule, with perianth tube becoming thin and sometimes splitting at fruit maturity. Flowering May–June.

All measurements above are for fresh, not pressed, specimens, collected in the relatively dry year of 2006. Measurements might be somewhat greater in a wetter year. The flower parts in dried specimens shrink by roughly 10%. The ranges in the measurements above are exactly the ranges of our measured values; it is expected that the true population range is somewhat greater.

Type: USA, California, Riverside Co., Santa Ana Mountains, Santa Rosa Plateau region: Clay Hill, 0.55 km south-southwest of the northernmost high point of the Mesa de Burro; 33.52927° N, 117.24857° W [NAD27]; 580 m elevation; 15 June 2006, *T. Chester, W. Armstrong, K. Madore 927* (holotype UCR; isotypes RSA, SD).

Paratypes: All from USA, California, Santa Ana Mountains. Riverside Co. specimens: Elsinore Peak, 0.3 km southwest of the Peak, 33.60049 decimal degrees N, 117.34514 degrees W [NAD27], 1045 m elevation, 10 June 2006, *T. Chester, W. Armstrong 918 (UCR),* 15 May 1992, *S. Boyd 7385 (RSA, UCR)*; Mesa de Burro, 23 June 1983, *R. Gustafson and G. Wallace 2716 (RSA),* 25 May 1977, *C. Davidson 5639 (RSA),* 0.4 km west of the north end, 17 May 1988, *S. J. Myers s.n. (UCR)*; Mesa de Colorado, 18 May 1985, *R. Thorne et al. 60644 (RSA)*, 27 May 1960, *E. Lathrop 5221 (RSA)*, Via Volcano Road just north of Avocado Mesa Road, *T. Chester, W. Armstrong 921 (UCR)*; Avenaloca Mesa, west side, northwest of intersection of Corona Cala Camino and Avocado Mesa Roads,

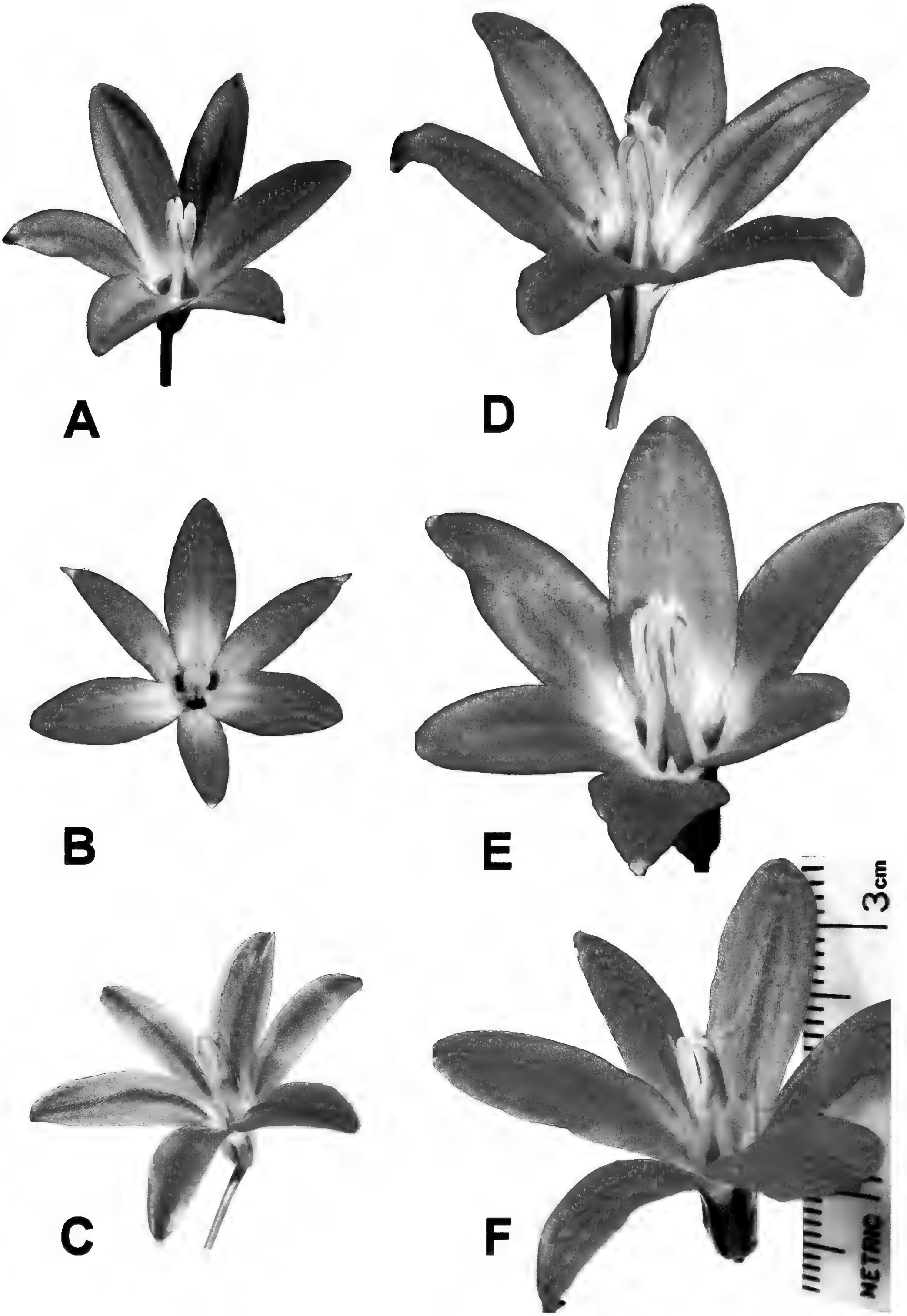

FIG. 1. Comparison of flowers of *B. santarosae* with *B. orcuttii, B. filifolia* and *B. filifolia X B. orcuttii.* (A) *B. orcuttii* (B) *B. filifolia* (C) *B. filifolia X B. orcuttii.* (D–F) *B. santarosae*. The flowers shown in D and E are from the same corm. All flowers are to the scale shown in F, and are shown in the same proportion to each other as for the median-size flower for each taxon.

33.49379° N, 117.33178° W [NAD27], 720 m elevation, 22 June 2006, *T. Chester, W. Armstrong 934 (UCR)*. San Diego County: south flank of Miller Mountain, about upper portion of Miller Canyon, ~730 m, 6 May 1992, *S. Boyd et al. 7289, 7304B* (RSA), *7304A (SD)*.

Epithet etymology, pronunciation, and common name. The epithet is for the Santa Rosa Basalt closely associated with this species. The suggested pronunciation is *san-tuh rose' ee* (U.S.), or *san-tuh rose' eye* (European). The suggested common name is *Santa Rosa Basalt Brodiaea.*

Distribution

Brodiaea santarosae is found only in a unique location in southern California, an area of low topographic relief that was flooded by the Santa Rosa Basalt 8–11 million years ago. Its range mostly, but not entirely, separates the populations of *B. filifolia* and *B. orcuttii.*

Fig. 2A shows the geographic range of these three species, along with the estimated minimum original extent of the basalt. Populations of *B. orcuttii* are found entirely to the south and southeast of the basalt. Populations of *B. filifolia* are found mostly to the north and west of the basalt, with just a few occurrences to the south, and only one population within the basalt area. That population, at the Mesa de Colorado, occurs at the biggest vernal pool, in heavily-leached dark vernal pool soils unlike the reddish basalt-derived soil elsewhere on the basalt; it is not accompanied there by *B. santarosae.*

The Santa Rosa Basalt has been dated as 8–11 million years old (Hull and Nicholson 1992; Hawkins 1970; D. Krummenacher, cited in Kennedy 1977). It formerly covered an area of at least 500 km^2 (Kennedy 1977), from Elsinore Peak on the north, to the Murrieta Hogbacks and Oak Mountain on the east, to somewhere south of the Mesa de Colorado on the south, and to the area of Miller Mountain on the west. This is a minimum extent, estimated simply by taking the surviving patches of basalt and assuming basalt originally was continuous between them. Erosion has removed at least 97% of the original basalt area; the basalt now covers only disjunct areas of about 15 km^2 (within a region of approximately 40 km^2) plus a few very small patches such as the two patches at Elsinore Peak 11 km distant.

We include the "Basalt of Elsinore Peak", dated only as "Miocene" (Morton et al. 1999), as part of the Santa Rosa Basalt. Because these basalts most likely derived from the same or very similar source, and are from the same time period, they are highly likely to be substantially the same, and are treated as such here.

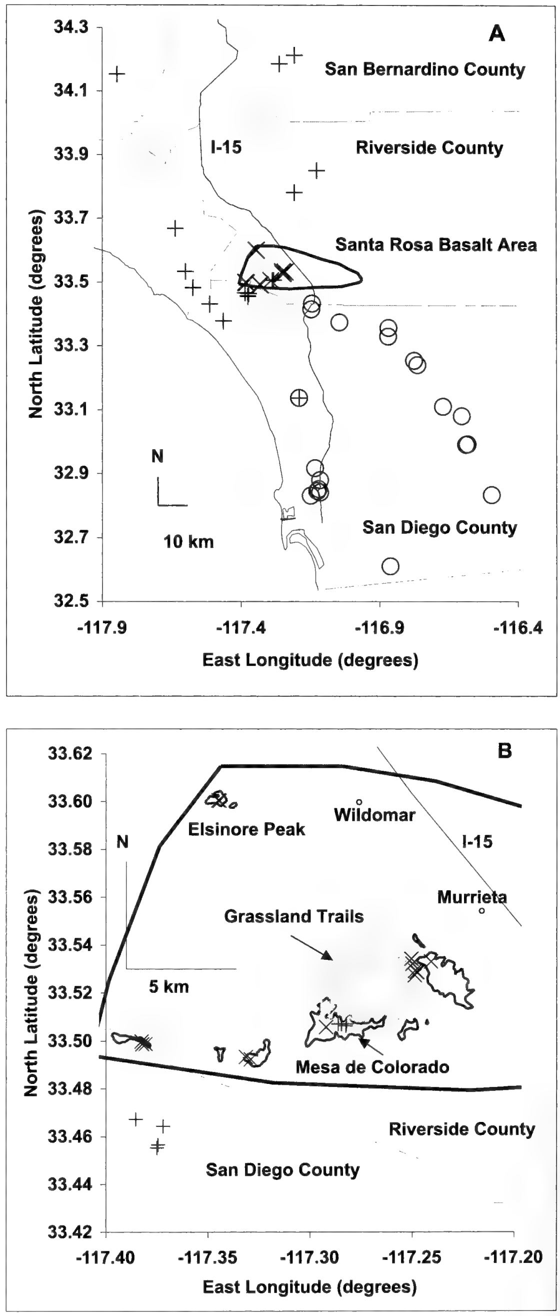

FIG. 2. Geographic distribution of *B. filifolia* (+), *B. santarosae* (X), and *B. orcuttii* (O) in southern California, USA from vouchers, both ours and ones at RSA, SD and UCR verified by the authors. The minimum original extent of the Santa Rosa Basalt is outlined using the present position of the Basalt. A. Map showing all populations. B. Expanded-scale map showing remaining areas covered by Santa Rosa Basalt (black outline areas) and trails of the Santa Rosa Plateau Ecological Reserve in grassland (light gray).

Fig. 2B shows the largest remaining areas of the basalt, along with all vouchered locations of *B. santarosae* and *B. filifolia* in that area. Voucher locations of most *B. santarosae* specimens are not precise; locations such as *Mesa de Burro* have been arbitrarily placed on the Mesa. Most of the extant basalt is on the mesas of the Santa Rosa Plateau, not all of which have yet been surveyed for these species. All Santa Rosa Basalt areas surveyed to date contain *B. santarosae*.

Perhaps the most remarkable feature of *B. santarosae* is that every population we surveyed grows in soils derived from the Santa Rosa Basalt. Every surveyed population except one, and all vouchers we determined as *B. santarosae*, were from soils underlain by the Santa Rosa Basalt as mapped in Kennedy (1977). The exception was the population immediately west of the Mesa de Burro. Although the basement rock there is mapped as metasedimentary, the soil had abundant basalt rocks within it and on its surface, remaining from the geologically-recent past when the Santa Rosa Basalt was still intact here. Thus this soil is derived, at least in part, from the basalt.

This distribution thus shows tremendous fidelity to the basalt areas, since both the populations and the major remaining basalt areas (not including the unsurveyed Oak Mountain) span a distance of 15 km by 15 km, yet both *B. santarosae* and the basalt only cover almost the identical ~7% (15 km^2/225 km^2) of that area.

This coincidence is not due to habitat considerations; there are extensive grasslands inhabited by *B. terrestris* Kellogg subsp. *kernensis* (Hoover) T. Niehaus outside the basalt areas. No other populations of *B. santarosae*, *B. filifolia*, or *B. orcuttii* have been documented even though those grasslands have been intensely studied. The first and third author surveyed the grassland trails of the Santa Rosa Plateau Ecological Reserve shown in Fig. 2B in 2001–2006; Lathrop and Thorne (1985) surveyed most of the area shown in Fig. 2B south of Murrieta; Boyd et al. (1995) surveyed the rest of the area shown in Fig. 2B; and there have been numerous surveys for residential development.

Thus, it is likely that there are no other populations of *B. santarosae* other than those shown, except for more populations in the basalt areas themselves. In particular, Redonda Mesa and Mesa de la Punta may contain additional populations. In addition, there are a few locations that have small remnants of the Santa Rosa Basalt, not shown on the map, such as the Murrieta Hogbacks and Oak Mountain. These areas should be searched for *B. santarosae*. It is also possible that small populations of *B. santarosae* might occur in drainages from basalt areas, carried there by runoff.

Key to the Species of *Brodiaea* in Southern California

This key is an artificial key to separate all species of *Brodiaea* in mainland southern California. In this key and subsequently in this paper, the properties of the staminode refer only to its free portion and do not include the lower continuation of the staminode that is fused to the outer perianth.

1 Staminodes 0 in all flowers . . . . *B. orcuttii*
1' Staminodes present in 90–100% of flowers . . . (2)
2 Staminodes oblong to rectangular in outline, tapered only near tip if at all . . . . (3)
2' Staminodes filiform or uniformly tapered from base to tip . . . . (4)
3 Staminodes generally erect, edges flat to inrolled, sometimes hooded, generally purple. . . . . *B. terrestris* ssp. *kernensis*
3' Staminodes recurved, edges flat, not hooded, pointed at tip, generally white; Mission Trails Regional Park . . *B. elegans* Hoover subsp. *elegans*
4 Filaments 0–1.5 mm; staminodes 1.0–4.5 mm long, reflexed against perianth . . . . *B. filifolia*
4' Filaments 2–8 mm; staminodes 0.0–7.0 mm long, recurved to erect. . . . . (5)
5 Perianth length 19–24 mm; style 8.0–9.5 mm; ovary 4.0–5.0 mm; anther 5.0–5.5 mm; San Marcos . . . .*B. filifolia* × *B. orcuttii*
5' Perianth length 24–36 mm; style 10.5–17.0 mm; ovary 3.5–8.2 mm; anther 5.4–8.9 mm; Elsinore Peak to Miller Mountain . . . . *B. santarosae*

Because only three specimens of *B. filifolia* × *B. orcuttii* are known, the range of measurements for it in the above key will require slight extensions as more specimens are found. However, the principal component analysis presented below indicates that those extensions will be much smaller than the differences from *B. santarosae.*

Phenetic Analysis of *Brodiaea Santarosae* and Other *Brodiaea* Species in Southern California

Data and Analysis Methods

We surveyed, photographed, and sampled populations from the following areas, mapped in Fig. 2A, specifically for this analysis, on 1, 4, 5, 10, 13, and 22 June 2006. The species determination for each specimen was made later from the analysis in this paper. Numbers in parentheses are collection numbers of Chester et al. *B. filifolia*: Santa Rosa Plateau Ecological Reserve (SRPER): Vernal Pool Trail near Main Pool (909); San Marcos (912); San Mateo Canyon Wilderness: Mud Canyon 1 (920, 933), Mud Canyon 2 (924). *B. filifolia* × *B. orcuttii*: San Marcos (917, 936). *B. orcuttii*: Miramar (915); Cuyamaca Lake (916); Tierra Santa (935). *B. santarosae*: SRPER: Clay Hill Area (910–911,

925–930), Via Volcano Road (921); Elsinore Peak (918); Avenaloca Mesa (934). *B. terrestris* subsp. *kernensis*: Elsinore Peak (919); SRPER: Via Volcano Road (922).

Mud Canyon is the informal name used for the drainage in the San Mateo Canyon Wilderness Area near Devil Canyon that contains Mud Springs. Mud Canyon 1 is a drainage from a fairly large upstream meadow area. Mud Canyon 2 is a small grassy area a few hundred feet south of Mud Canyon 1.

In each area, we photographed the full range of variation seen in the flowers, and we selected 5–10 inflorescences or flowers to measure in detail. The samples were selected mostly geographically, from the edges of each area and from the center, in order to avoid having multiple samples from the same clonal population. (*Brodiaeas* often reproduce by corms, and hence the population in a small area is often clonal.) Samples were also taken of extreme members of the population if the geographic sampling did not encompass all the variation seen in the population. The one exception to the above sampling was on the 18 June 2006 visit to San Mateo Mud Canyon 1, where we intentionally sampled only the largest flowers from the *B. filifolia* population in an attempt to discover any population intermediate to *B. santarosae*. (Later analysis showed no intermediates were found.)

For comparison purposes, especially to study any possible hybridization, we also used data collected in 2005 from the SRPER for fresh samples of *B. terrestris* subsp. *kernensis*.

Fourteen independent characteristics were measured for each fresh flower before pressing, in addition to the scape and bract length for each inflorescence. In addition, all herbarium samples of "*B. filifolia*", "*B. orcuttii*", and "*B. filifolia* × *B. orcuttii*" from RSA and SD were examined and measured for all quantities visible on each specimen, and re-determined.

These characteristics were then analyzed directly and with principal components analysis.

Principal Components Analysis. The measurements of seven floral parameters (perianth lobe, perianth tube, filament, anther, ovary, style, and staminode) were analyzed for principal components, with the results separated by geographic populations in Fig. 3.

We removed the mean from each floral parameter and then computed the principal components in two ways, once dividing each parameter by its standard deviation and once without such division. Since the resulting plots were essentially identical except for scale (r^2=0.95 for PCA1 and 0.96 for PCA2), we present here the version without such scaling which allows the coefficients to be more easily interpreted. The scale factors that will closely give the other version are given in the caption for Fig. 3.

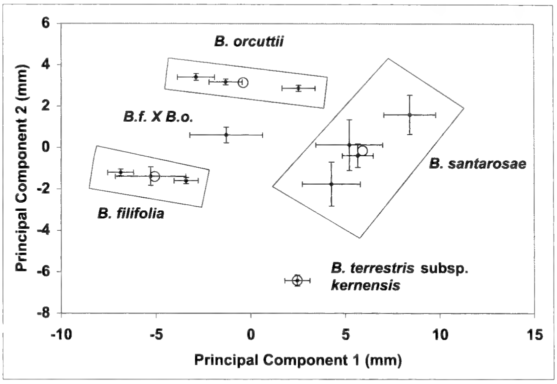

FIG. 3. Principal Components Analysis of floral parameters not scaled by standard deviation. The mean values with their one-standard deviation error bars are shown for the eleven geographically-distinct populations given in Table 1. Rectangles delineate individual taxa with more than one population; circles denote the mean for each taxon. To convert to PCA values from floral parameters scaled by standard deviation, multiply PCA1 by 0.389 mm^{-1} and PCA2 by 0.425 mm^{-1}.

Results of Analysis of Characteristics of the *Brodiaea* Species

The coefficients of the first two principal components (PC1 and PC2) are given in Table 1, along with the variation in PC2 contributed by each variable. These two components accounted for 89% of the total variance in the data.

Principal Component 1 is a length parameter, essentially a scale factor times the perianth length plus the portion of the length of the floral parts that is correlated to the perianth length. Principal Component 2 is essentially a scale factor times the lengths of the filament plus the style minus the perianth tube minus the perianth lobe minus the staminode, where the staminode contributes roughly twice the variation of the other parameters. The variable staminodes of *B. santarosae* account for most of the spread in values of PC2 for that taxon. Table 1 also shows the variation in PC2 contributed by each parameter.

TABLE 1. COEFFICIENTS FOR PRINCIPAL COMPONENTS PC1 AND PC2, AND VARIATION IN PC2, BY PARAMETER.

Parameter	PC1	PC2	PC2 Variation (mm)
Tube	0.19	−0.36	−3.28
Lobe	0.70	−0.16	−3.46
Filament	0.36	0.46	3.73
Anther	0.18	0.02	0.11
Ovary	0.21	−0.15	−1.00
Style	0.51	0.22	2.94
Staminode	0.09	−0.76	−6.64

The error bars in Fig. 3 were computed by dividing the population standard deviation for each species by $(n-1)^{1/2}$, where n is the number of individuals in each population. Note that some populations, such as *B. filifolia* and *B. filifolia* × *B. orcuttii* from San Marcos, are represented by only three specimens, which accounts for some of the larger error bars.

Fig. 3 shows four distinct taxa that are nearly equally distant from each other, the three distinct clusters denoted by labeled rectangles and the point corresponding to *B. terrestris* subsp. *kernensis*. The *B. filifolia* × *B. orcuttii* specimens plot almost exactly intermediately between the parent species, as expected for F1 hybrids. Since these specimens are found only in the single location where the parent species occur together, the evidence for their hybrid origin is strong.

The separation of the taxa in Fig. 3 demonstrates that *B. santarosae* is a taxon as distinct as any of the other three taxa, with characteristics not intermediate to any of those three taxa. In particular, these specimens are not direct hybrids of *B. filifolia* and *B. orcuttii*, nor are they part of any hybrid swarm between those species. Our discovery of clear hybrids between *B. filifolia* and *B. orcuttii*, from the only location where the populations overlap, confirms these conclusions.

The clusters denoted by the labeled rectangles in Fig. 3 are robustly defined. Note in particular the very small error bars on the PC2 values for all taxa except *B. santarosae;* within each of those clusters, all populations show extremely good concordance for PC2 in Fig. 3, reflecting the uniform staminodes of each taxon. The populations of *B. santarosae* also show good concordance, with each having significant spreads in the values of PC2, reflecting the staminode variability of that species being consistent between populations.

For both PC1 and PC2, the mean of each population is consistent with the corresponding species mean (Fig. 3), except for the *B. orcuttii* population with the highest value of PC1. That population (San Marcos) is 3.3 standard deviations away from the species mean value. Since PC1 is essentially the perianth length, this simply means that the San Marcos flowers in our sample were significantly larger than the other two populations from Miramar and Cuyamaca Lake.

Although the San Marcos specimens possessed somewhat-larger flowers, they are otherwise consistent with the other two *B. orcuttii* populations in all respects. In particular, they have the distinctive properties of *B. orcuttii* described below, including the complete absence of staminodes. Herbarium specimens show a much smaller separation of San Marcos flowers from the other two populations in other years, indicating that the apparent difference in our samples was either sampling variation or perhaps related to the unusual rainfall pattern in 2006. For additional detail, see Chester et al. (2007).

Comparison of Individual Characteristics of *Brodiaea* Species in Southern California

Measured ranges for each parameter for each species are given in Table 2, along with the number of samples measured. We did not include *B. elegans* or *B. kinkiensis* in the analysis here since they do not come into the geographic range of any southern California *Brodiaea* except for *B. terrestris* subsp. *kernensis*, and we therefore didn't sample them for this analysis. (For this analysis, we treat southern California specimens determined as *B. jolonensis* Eastw. as *B. terrestris* subsp. *kernensis.* They have numerous differences from specimens of *B. jolonensis* from the type locality of Jolon, CA, and are nearly identical to specimens of *B. terrestris* subsp. *kernensis.*) The sampling of *B. terrestris* subsp. *kernensis* was not extensive enough to give the full range for its parameters, especially from other locations.

Brodiaea santarosae showed the following substantial differences from *B. filifolia* and *B. orcuttii*:

(1) It had larger flowers and larger floral parts. The median *B. santarosae* flower was 40% larger than the median *B. filifolia* and *B. orcuttii* flower. Only a small percentage of *B. filifolia* and *B. orcuttii* flowers were larger than the *smallest B. santarosae* flower.
(2) The anther, ovary and style lengths of *B. santarosae* were all markedly longer than those for *B. filifolia* and *B. orcuttii*. There was almost no overlap at all for anther lengths, and only a small overlap for the other lengths.
(3) The inflorescence bract and pedicel lengths for *B. santarosae* were typically much longer than those of *B. filifolia* and *B. orcuttii*. Two-thirds of the bract lengths for *B. filifolia* and *B. orcuttii* were shorter than 6 mm; none of the bracts of *B. santarosae* were that short. All pedicels of *B. filifolia* and *B. orcuttii* were shorter than 75 mm, but over one third of the pedicels of *B. santarosae* were longer than 75 mm.
(4) The peduncle lengths for *B. santarosae* were also much longer than those of *B. filifolia* and *B. orcuttii*. However, this may simply be a consequence of the habitat difference. *B. santarosae* grows in areas with abundant tall non-native grasses, whereas the other two species grow in areas without as much such cover.

In the rest of this section, we compare all four species and give those properties in which one or more species significantly differed at close to or

TABLE 2. MEASURED CHARACTERISTICS, IN mm. Min = minimum, Med = median, and Max = maximum. Values in bold type indicate an extension to the parameter range in Keator (1993). The actual range of values for *B. terrestris* subsp. *kernensis* is larger than reported here, since we only used a single sample of plants from the Santa Rosa Plateau to compare with the other species.

Characteristic	*B. filifolia*				*B. orcuttii*				*B. santarosae*				*B. terrestris* subsp. *kernensis*			
	#	Min	Med	Max	#	Min	Med	Max	#	Min	Med	Max	#	Min	Med	Max
Peduncle	23	**45.0**	**158.0**	275.0	30	**13.0**	107.0	**325.0**	12	88.0	257.5	360.0	14	65.0	162.0	**330.0**
Bracts	23	5.0	6.0	8.0	32	3.5	6.0	8.0	14	6.5	8.5	11.0	14	8.0	9.5	15.0
Pedicel	38	13.0	30.0	**59.0**	43	**5.0**	38.0	**60.0**	30	18.0	56.0	107.0	15	25.0	39.0	**71.0**
Perianth tube	38	**4.5**	6.7	**9.0**	43	4.0	**6.0**	**10.0**	30	6.0	8.3	11.3	15	**8.2**	**10.0**	**13.2**
Perianth lobes	38	**7.2**	12.9	**20.0**	43	**11.4**	15.2	**22.0**	30	15.4	19.5	29.5	15	**14.9**	19.0	**21.8**
Perianth	38	**13.2**	19.5	**28.0**	43	17.0	21.0	**32.0**	30	24.0	28.1	36.5	15	**23.5**	30.0	**35.0**
Filament	38	**0.0**	**0.4**	**1.5**	43	**3.9**	5.2	**7.9**	30	2.4	5.8	8.2	15	1.2	3.0	4.0
Anther	38	**2.8**	4.5	**6.0**	43	4.0	5.2	**6.6**	30	5.4	6.8	8.9	15	**4.3**	5.1	**6.8**
Ovary	38	**2.9**	4.5	**7.2**	42	**2.7**	5.0	**7.1**	30	3.5	7.0	8.2	15	**6.5**	**7.6**	**9.2**
Style + stigma	37	**4.5**	6.3	**9.1**	42	**5.8**	9.0	**15.1**	30	10.5	13.0	17.0	15	7.0	8.0	**10.0**
Width anther axis	29	0.1	0.5	1.0	40	0.2	0.5	1.0	25	0.3	0.8	1.1	15	0.2	0.9	1.0
Width of anther sac	29	0.2	0.5	0.8	40	0.2	0.5	0.8	25	0.2	0.6	0.9	15	0.5	0.8	0.9
Perianth base width	21	1.9	2.3	3.1	42	2.1	2.7	3.2	24	2.0	2.9	3.9	7	2.0	2.5	2.8
Upper pedicel width	21	1.0	1.0	1.2	43	1.0	1.2	1.5	24	1.1	1.4	1.9	7	1.3	1.6	2.0
Staminodes (free portion)	38	**1.0**	2.5	**4.2**	43	0.0	0.0	0.0	30	0.0	3.3	7.0	13	4.8	7.5	8.8
Staminodes (including fused portion)	21	2.4	3.5	5.0	42	1.0	2.0	4.0	30	1.5	5.1	8.5	15	8.0	10.0	11.7
Distance from top of anthers to top of style (anthers above style positive)	31	−2.0	1.0	2.6	42	−1.8	2.0	5.2	26	−1.4	1.0	3.0	3	−0.2	1.0	2.2

exceeding the 95% confidence level (with a difference more than two standard deviations). Plots, histograms, and additional information are given in Chester et al. (2007).

Habitat. The habitats of the four species are distinct. *B. filifolia* and *B. orcuttii* are confined to the wettest areas such as flat streambeds, benches along streambeds, and vernal pool areas. *B. terrestris* subsp. *kernensis* and *B. santarosae* are less moisture-dependent. *B. terrestris* subsp. *kernensis* grows in many habitats, but generally does not occur in the wettest areas preferred by *B. filifolia* and *B. orcuttii*. It grows in drier drainages and along trails and roads in flattish areas.

Brodiaea santarosae grows in many habitats as well, including next to vernal pools, but can grow in drier locations than even *B. terrestris* subsp. *kernensis*. Surprisingly, *B. santarosae* even grows in disturbed areas such as Waterline Road next to the Mesa de Burro. That area was completely dug up to install a water main, and *B. santarosae* grows abundantly in the disturbed soil on top of the water pipe, as well as in roadside berms.

There is only one known occurrence of *B. filifolia* within the range of *B. santarosae*, on the Mesa de Colorado immediately surrounding the largest vernal pool. The area in which it grows was part of that pool for ~75 years, when the outlet of the pool was dammed to raise the level of the pool. The soil in that area is heavily leached, and does not have the red color of the surrounding basalt-derived soil. *B. santarosae* is not found on that vernal pool soil, only in the red basalt soil elsewhere on the Mesa de Colorado.

Of course, the most remarkable difference in habitat is the restriction of *B. santarosae* to basalt soil in areas on or near the Santa Rosa Basalt.

Peduncle and bract lengths. Histograms of these two parameters (Fig. 4) each showed two distinct patterns: *B. filifolia* and *B. orcuttii* had similar histograms that peak at shorter values, and *B. santarosae* and *B. terrestris* subsp. *kernensis* had similar histograms that peak at longer values. For example, 60% of the peduncles for *B. filifolia* and *B. orcuttii* were less than 150 mm, but only 27% of the peduncles for the other two species were that short. Even more dramatically, 65% of the bract lengths for *B. filifolia* and *B. orcuttii* were less than 6 mm, but none of the bract lengths for the other two species were that short.

Although it is possible that the peduncle length further distinguishes *B. santarosae* from *B. filifolia* and *B. orcuttii*, we suspect the peduncle length is subject to environmental modification by the height of the immediately-neighboring plants, which in turn derives from the different habitats of these species. Peduncles are shorter where there are few neighboring plants, and longer where the plant is surrounded by tall annual non-native grasses. Both *B. filifolia* and *B. orcuttii* are found in habitats that largely exclude non-native annual grasses, whereas *B. terrestris* subsp. *kernensis* and especially *B. santarosae* are found in drier habitats that favor those grasses. Supporting our suspicion, the range of peduncles is essentially the same for every species even though the histograms are different, implying that each species grows its peduncle long enough for its flowers to be out in the open.

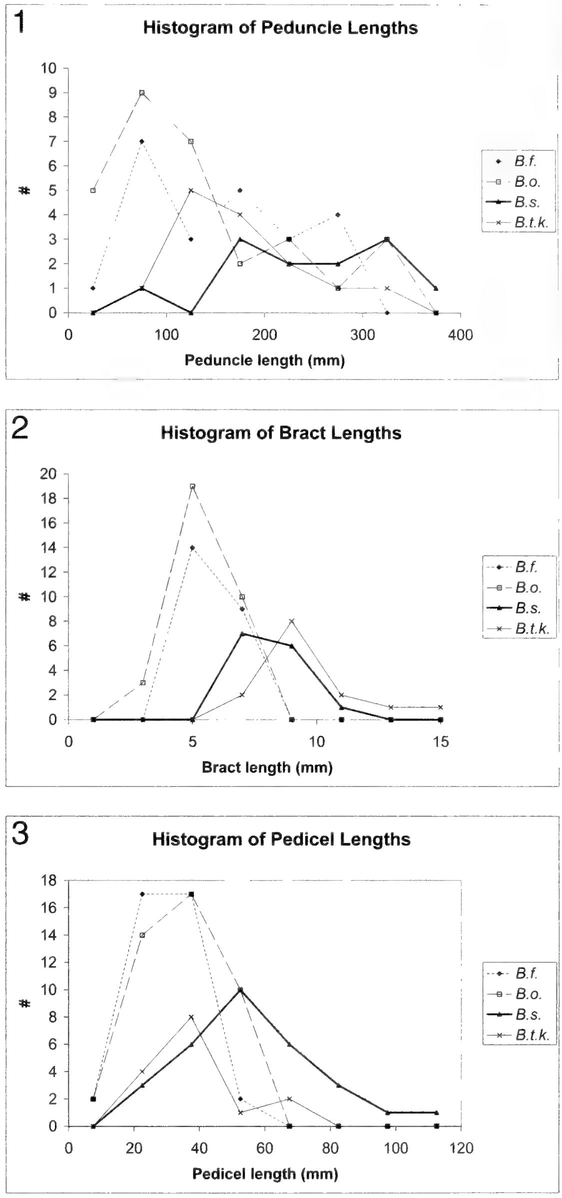

FIG. 4. Histograms of peduncle, bract and pedicel lengths for *B. filifolia* (*B.f.*), *B. orcuttii* (*B.o.*), *B. santarosae* (*B.s.*), and *B. terrestris* ssp. *kernensis* (*B.t.k.*).

The difference in bracts is more fundamental since the range for bract lengths is very different among the species; there seems to be a firm upper

TABLE 3. SCALING OF FLORAL CHARACTERISTICS WITH PERIANTH LENGTH: SLOPE AND STANDARD DEVIATION. Slope values in bold type indicate characteristics significantly larger than for the other species; values in italics indicate significantly-smaller characteristics.

Characteristic	*B. filifolia*	*B. orcuttii*	*B. santarosae*	*B. terrestris* subsp. *kernensis*
Perianth tube	**0.20** ± 0.04	**0.31** ± 0.05	*0.05* ± 0.07	0.28 ± 0.07
Perianth lobes	0.80 ± 0.04	0.69 ± 0.05	0.95 ± 0.07	0.72 ± 0.07
Filament	*0.09* ± 0.02	**0.19** ± 0.03	**0.26** ± 0.09	0.11 ± 0.06
Anther	0.13 ± 0.03	0.13 ± 0.02	0.17 ± 0.04	0.16 ± 0.03
Ovary	0.19 ± 0.04	0.19 ± 0.03	−0.01 ± 0.06	0.14 ± 0.07
Style + stigma	0.31 ± 0.05	0.41 ± 0.05	0.37 ± 0.06	*0.17* ± 0.04
Staminodes (free portion)	0.04 ± 0.03	0.00 ± 0.00	−0.19 ± 0.14	0.16 ± 0.07

limit for the bract length of *B. filifolia* and *B. orcuttii*.

Pedicel lengths. As for the peduncle and bract lengths, *B. filifolia* and *B. orcuttii* had a similar pattern with histograms that peak at shorter values (Fig. 4). However, *B. terrestris* subsp. *kernensis* had a histogram shifted only slightly to larger values, whereas *B. santarosae* had a histogram shifted dramatically to larger values. For example, all pedicels of *B. filifolia* and *B. orcuttii* were less than 60 mm, but 37% of the pedicels of *B. santarosae*, and 13% of the pedicels of *B. terrestris* subsp. *kernensis*, were greater than 60 mm.

Floral parameter lengths. Analysis of seven floral parameters, plotted against perianth length and analyzed with linear regression, revealed that every floral parameter for every species scaled with the perianth length with two exceptions. First, the staminodes for every species except *B. terrestris* subsp. *kernensis* did not scale with perianth length. The staminodes for *B. terrestris* subsp. *kernensis* scaled with perianth length much the same as every other non-corolla floral parameter, which had slopes of 0.11 to 0.17. (This slope value means that for every 10 mm enlargement of the corolla, the other part lengthens by 1.1 to 1.7 mm on average.) All of the other species had fitted slopes consistent with zero within two standard deviations. (The slope was of course exactly zero for *B. orcuttii* since its staminode length is always zero.) The fitted slope of the staminode length for *B. santarosae* was actually negative with perianth length; i.e., there was a tendency for the maximum staminode length to *decrease* with increasing perianth length. However, the slope value was only 1.4 times its standard deviation, consistent with zero.

Second, the perianth tube and ovary length for *B. santarosae* did not scale with perianth length. It is tempting to say that these values have simply reached their maximum values for the large flowers of this species, but both characteristics had a significant positive slope for *B. terrestris* subsp. *kernensis*, which had equally large flowers. These two exceptional traits add to the suite of characters that make *B. santarosae* distinctive.

The scaling with perianth length for the other floral parameters, given in Table 3, was generally consistent between all species, with the following exceptions: the tube for *B. filifolia* grew more slowly with perianth length than did the tube for *B. orcuttii*, a difference of 1.7 standard deviations ($P = 0.09$ due to chance); the filament length for *B. filifolia* grew more slowly with perianth length than did the filament lengths for *B. orcuttii* and *B. santarosae*, differences of 2.9 standard deviations ($P = 0.004$) and 1.9 standard deviations ($P = 0.06$), respectively; and the style (including stigma) length for *B. terrestris* subsp. *kernensis* grew more slowly with perianth length than did the styles for the other species, differences of 2.1–3.9 standard deviations ($P = 0.04$–0.0001).

Table 4 gives the mean values and standard deviation of the mean for the floral characteristics. Significantly-larger mean values are in bold type; significantly-smaller values are in italics; the differences here range from 4.4-10 standard deviations ($P<10^{-5}$). Six of the seven characteristics of *B. filifolia* and *B. orcuttii* were significantly-smaller than at least one of the other two species; in contrast, six of the seven characteristics of *B. santarosae* were significantly-larger than at least one of the other two species. Interestingly, *B. terrestris* subsp. *kernensis* had three significantly-smaller values and four significantly-larger values. In addition, the width of the anther axis tissue for *B. terrestris* subsp. *kernensis* was 0.5–0.9 mm and never became as narrow as the minimum value for each the other species of 0.2 mm.

CONCLUSIONS AND DISCUSSION

Brodiaea santarosae merits designation at the rank of species. The plants are taxonomically distinct in a number of significant features from all other *Brodiaea* species, and in fact are among the most distinctive *Brodiaea* species. The plants are not direct hybrids of *B. filifolia* and *B. orcuttii*, nor are they part of a hybrid swarm between those species. The plants form a homogeneous population with a well-defined geographic range. Further, as is often the case for many recently-recognized species, this species is

TABLE 4. FLORAL CHARACTERISTICS MEAN AND STANDARD DEVIATION OF THE MEAN, IN mm. Values in bold type indicate characteristics significantly larger than for at least one other species; values in italics indicate significantly-smaller characteristics.

Characteristic	*B. filifolia*	*B. orcuttii*	*B. santarosae*	*B. terrestris* subsp. *kernensis*
Perianth tube	*6.7* ± 0.2	*6.1* ± 0.2	**8.3** ± 0.2	**10.2** ± 0.3
Perianth lobes	*13.5* ± 0.4	*15.8* ± 0.4	**20.0** ± 0.6	**19.2** ± 0.7
Filament	*0.5* ± 0.1	**5.4** ± 0.1	**5.6** ± 0.3	*2.7* ± 0.2
Anther	*4.6* ± 0.1	*5.3* ± 0.1	**6.8** ± 0.1	*5.4* ± 0.2
Ovary	*4.5* ± 0.1	*5.2* ± 0.2	**6.8** ± 0.2	**7.6** ± 0.2
Style + stigma	*6.6* ± 0.2	*9.4* ± 0.3	**13.1** ± 0.3	*8.1* ± 0.2
Staminodes (free portion)	2.6 ± 0.1	*0.0* ± 0.0	3.3 ± 0.4	**7.5** ± 0.2

closely associated with an unusual soil type, the unique area in southern California defined by the Santa Rosa Basalt. The discovery of this species supports the speculation in Kruckeberg (2006) that "*most new species will be in places ... with kooky soils..in such remote places ... as ... out of the way places in southern California*".

Eleven separate characteristics distinguish *B. santarosae* from the two species with which it has previously been confused, *B. filifolia* and *B. orcuttii.* Five of those 11 characteristics also distinguish *B. santarosae* from *B. terrestris* subsp. *kernensis*: its staminode properties, anther and style lengths, and the lack of scaling with perianth length of the perianth tube and ovary. The other six characteristics are the lengths of the inflorescence bracts, pedicels, perianth tubes, perianth lobes, ovaries, and its habitat.

The association with the Santa Rosa Basalt makes *B. santarosae* an interesting species for further study. Raven and Axelrod (1995) speculate that genera with many species endemic to the California Floristic Province, such as *Brodiaea*, were in the area long before the climate transitioned to a Mediterranean one without summer rainfall at about five million years ago or so. Such taxa then gradually adapted to the lack of summer rainfall, and radiated to form new species as new habitats became available (Niehaus 1971).

The Basalt is accurately dated as 8–11 million years old (Kennedy 1977), and hence was present long before the climate changed. It is possible that *B. santarosae* originated before the climate change as well. DNA studies may be able to elucidate the evolutionary relationship between *B. santarosae* and its neighboring species with small geographic ranges, *B. filifolia* and *B. orcuttii.* Niehaus (1971) speculated that *B. filifolia* and *B. orcuttii* were young species from their diminished staminodes and their association with soils that have only appeared recently.

Brodiaea filifolia occurs primarily on "recent alluvial soil" and *B. orcuttii* occurs in the western part of its range on "old terrace soils which were previously submerged by the sea but recently became available" (Niehaus 1971). Both of these soils appeared much later than the Basalt soil. Most alluvial soil on which *B. filifolia* is found is mapped as Quaternary (California Division of Mines and Geology 1962, 1966), although similar soil probably appeared earlier, perhaps two million years ago. The old terrace soils on which *B. orcuttii* is found are considered to have emerged only in the last one million years (Abbott 1999). However, Niehaus was apparently not aware of the populations of *B. orcuttii* in the Cuyamaca Mountains. Although that terrain has been present for a much longer time (Norris and Webb 1976), it isn't known whether *B. orcuttii* only recently spread to that terrain or originated there.

Future evolutionary studies of these three *Brodiaea* species may thus add new information to the evolution of the California flora. In contrast, the much-studied serpentine habitat, with its ~285 endemic taxa (Kruckeberg 2006) including *B. pallida* and *B. stellaris*, appeared after the shift to a Mediterranean climate. That habitat is less-accurately dated as having emerged in "*the late Pliocene and early Quaternary*" (Raven and Axelrod 1995), sometime more recently than about 5 million years ago.

The geographically-separate populations of *B. santarosae* may also allow DNA studies to give a minimum age of this species since those populations were last in full reproductive contact. An independent estimate of when those populations were isolated may also be possible from modeling the erosion of the Santa Rosa Basalt combined with estimates of the distance over which *Brodiaea* species can spread.

The association of *B. santarosae* with the Santa Rosa Basalt may imply that it is headed toward extinction in the near geologic future when the last trace of the basalt erodes away, unless it can adapt to non-basaltic soils. At least 97% of the Basalt has been eroded in the 8–11 million years since it formed. It will take much less than another 0.3 million years (3% of the previous erosion interval) to erode the remaining basalt, for the following two reasons. First, significant erosion of the basalt only began after the area was uplifted approximately 3.6 million

years ago (Gath et al. 2002). Second, the remnants are being eroded on all sides now, whereas most of the previous erosion was only along the edges of the formerly-intact basalt mass.

Conservation Status

Four of the known populations of *B. santarosae* are protected as part of the Santa Rosa Plateau Ecological Reserve and Cleveland National Forest. Another population, a large one on Avenaloca Mesa, is partially protected by the Nature Conservancy.

The discovery that the populations of *B. filifolia* in the San Mateo Canyon Wilderness Area and the Mesa de Colorado area are in fact pure *B. filifolia* adds two protected populations of *B. filifolia* to the list in U.S. Fish and Wildlife Service (2004). Formerly those populations were assumed to be hybrids and hence not as important as pure populations for the conservation of the species.

Acknowledgments

Steve Boyd was instrumental in this work, kindly sharing his detailed knowledge about locations and characteristics of *B. santarosae*, without which we could not have completed our fieldwork so quickly. We thank Rob Preston, Jane Strong, Andy Sanders and Steve Boyd for many helpful comments that have significantly improved this paper. We thank John Hunter, an anonymous referee, and Dale McNeal for constructive comments on the manuscript. Paula Knoll, Rob Hicks and Jim Adams also provided helpful comments. Voucher locations from UC, UCR and RSA, made available online by the Consortium of California Herbaria, were helpful in planning our fieldwork. Vouchers from RSA, SD and UCR were critical in determining the geographic range and the range of some properties for each species; we thank Judy Gibson and Jon Rebman for access to and hospitality at SD, Steve Boyd and Leroy Gross for the same at RSA, and Andy Sanders for the same at UCR. We thank Zach Principe for locations and information about the *B. santarosae* populations on Avenaloca Mesa. We thank Carole Bell for access to the Santa Rosa Plateau Ecological Reserve, and Bob Allen for help in collecting the type specimens there. We thank Ted St. John for information about the Santa Rosa Basalt and other possible occurrences of *B. santarosae* there. We thank Jean-Pierre Dujardin for his free program to compute the Principal Components. We thank Annette Winter for her valiant attempts to get a chromosome count from buds that were a bit too developed to yield results.

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REVIEW

Introduction to California Soil and Plants. Serpentine, Vernal Pools, and Other Geobotanical Wonders. By ART R. KRUCKEBERG. 2006. University of California Press, Berkeley, CA. 280 pp. $18.95. ISBN-13, 978-0-520-23372-0.

Serpentine Geoecology of Western North America. Geology, Soils, and Vegetation. By EARL B. ALEXANDER, ROBERT G. COLEMAN, TODD KEELER-WOLF, AND SUSAN P. HARRISON. 2007. Oxford University Press, New York, NY. 512 pp. $124.50. ISBN-13, 978-0-19-516508-1.

GEOECOLOGICAL EXTREMISM—OBSESSING ON GREEN ROCKS AND KOOKY SOILS

Serpentinite is the State Rock of California, a mineral associated with serpentine (Benitoite) is the California State Gem, the chromium and nickel in our drinking water and the asbestos in our air find their source in serpentine, something like 13% of California endemic plants are more or less restricted to serpentine soils, and now it turns out that the San Andreas fault may be sliding along a serpentine bed. This strange, rare, and often green product of the earth's mantle has a disproportionate influence on the environment that surrounds us. It is also beginning to have a disproportionate influence on the literature that surrounds us: a quick (and admittedly unscientific) search in Google Scholar turned up 36 hits for "serpentine" between 1950 and 1990, 5240 between 1991 and 1995, 8980 between 1996 and 2000, and 14600 between 2001 and 2005. The growing inventory of serpentine literature has been recently augmented by two new books treating the "geoecology" of serpentine rocks, soils, and biota in western North America: one for the layperson by the indomitable Art Kruckeberg, the other for the scientist, written by an all-star cast.

Kruckeberg's *Introduction to California Soil and Plants* is one of the latest supplements (Number 86, with six more already published since) to the venerable California Natural History Guides series published by UC-Press, and it is a worthy addition. It is the first of the series to treat soils, but it does so from a decidedly botanical viewpoint. This ends up skewing the book's pedologic treatment very strongly toward azonal (what Robert Ornduff called "kooky") soils, especially those developing on serpentine substrates. There is also consideration of—among other things—carbonates, dunes, and high water tables, but Kruckeberg's legendary expertise in serpentine geoecology leads unavoidably to a bias in this direction. If one is looking for a basic, even-handed treatment of different soils in California, this book will not fill the need. However, if one is looking for a lively and very engaging discussion of the very strong effects "kooky" soils can have on a region's flora, one would be hard-pressed to find a better, more readable, or more portable source.

For the most part, *Introduction to California Soil and Plants* is a pared-down reprise of Kruckeberg's classic *Geology and Plant Life*, published in 2002 by the University of Washington Press, but cheaper, in a sturdy pocketbook-sized paperback, and with color plates and photos (129 of them!). Obviously, it is also focused on California *per se.* I reviewed *Geology and Plant Life* for Madroño, and I have largely the same praise and criticisms for both books. For example, in this book as in his last, Kruckeberg still ignores the largely European roots of geoecology (what he calls "geo-edaphics"); he continues to (proudly!) fly the flag of "geologic primacy" in driving species distributions, when nearly everyone else on the planet has settled on "climatic primacy"; and he relies primarily on older literature (< 15% of the literature cited was published in the last ten years). Like the last book, I love the focus on tabular and graphic presentation of information, and I enjoy Kruckeberg's informal writing style—it conveys the author's absolute infatuation with the subject and it pulls the reader blissfully along—but every once in a while it can tie itself in knots. For example, from page 22: "A final word on the taxonomic status of rare or distinctive variant plant populations is the situation for edaphic races of mostly widespread species." Tighter editing could have cleared these things up, and one can hardly blame the author for a few first-draft shiners making it through.

Introduction to California Soil and Plants contains six chapters and an Introduction. As in *Geology and Plant Life*, I found certain chapters to be very good and others to be a tad unsatisfying. Perhaps I unfairly compare the current pocketbook contribution to its hardcopy "father", but I often found myself craving a little more explanation. Given the space constraints of the UC Natural History Guide format, this would have required reduction of other text, but this could have been accomplished with better editing. As in *Geology and Plant Life*, Kruckeberg's treatment of landform effects on plant life (Chapter 1) leaves something to be desired (in particular, there is too much listing of

species and too little discussion of causal processes), but his chapters on serpentine (Chapter 3) and "other strange soil-plant relationships" (Chapter 4) are good, concise summaries of the topics. Chapters 2 and 5 are short treatments of the soil-plant system ("geoedaphics") and historical biogeography, respectively. At the end of the book, Kruckeberg deals with human influences (Chapter 6) and then provides a short (10 page) annotated list of interesting places to view geoedaphics under the sun. For the layperson with an interest in serpentine soils and flora and a fancy for other geoecological novelties, *Introduction to California Soil and Plants* is a great buy ($18.95 in paperback), especially for planning roadtrips!

In *Introduction to California Soil and Plants,* Kruckeberg laments that conservation of serpentine habitats in California is "low to nonexistent". This concern is belied by information in *Serpentine Geoecology of Western North America*, which lists about 50 conservation areas on serpentine in California in Appendix F (and the list is incomplete). This is somewhat exemplary of the relationship between these two books—the first is wonderfully passionate and perhaps a tad too concise, the second is wonderfully dispassionate and—in places—a bit long-winded. Alexander et al.'s *Serpentine Geoecology of Western North America* was intended to appeal to the more scientific side of the serpentine audience, and it fills this role well. There is an amazing amount of information in this book: including some repeats (due to multiple reference sections), there are almost 41 pages of references, making this the most complete serpentine bibliography I have seen.

Serpentine Geoecology of Western North America includes an Introduction and 24 chapters organized into five parts: *Geology and Hydrology, Soils and Life in Them, Plant Life on Serpentine, Serpentine Domains of Western North America,* and *Social Issues and Epilogue.* There are also seven appendices. The authors' pedigrees are unassailable: Alexander is one of the most experienced field pedologists in the western United States, Coleman is the widely-recognized dean of serpentine geology, Keeler-Wolf is *the* expert in California vegetation classification, and Harrison may be the most published researcher in serpentine ecology worldwide. *Serpentine Geoecology of Western North America* sets out to assume the role of the go-to source for everything serpentine, and it does an admirable—if somewhat unbalanced—job.

Part I, which treats the geology and hydrology of serpentine in three chapters, is—for me—disappointingly brief. The geologic story of ultramafic rocks, their origins, and their improbable presence on the continents forms the fascinating core of the serpentine story, but Alexander et al. only dedicate two pages of text to this topic. More detail is provided in the chapters on mineralogy-petrology and water, but the total length of Part I is still only about 1/4 the length of the ensuing section on soils (34 vs. 122 pages). Some of the writing in Part I is awkward and difficult to follow, and there are many terms without adequate definition: e.g., Alpine-type serpentinites, crustal thinning, rootless slabs. Part I falls in that middle ground where laypeople may have trouble following the story, but experts will likely go elsewhere for more detail.

In contrast, Part II—*Soils and Life in Them*—is very long and very dense. Part II sometimes reads more like a soils textbook than a treatise on serpentine soil ecology: some of the information presented lacks a demonstrable link to the serpentine story, and a number of long tables could easily have been reduced or dropped. For example, the information in Table 5-1 (3 pages of soil carbon values) is duplicated in a subsequent figure and could have been dropped. Table 8-5 comprises seven pages of elemental concentrations in plants that could easily have been halved (and the clarity of presentation increased) by presenting means plus ranges for each species treated. The language of Part II also assumes a familiarity with soils terms, concepts and naming conventions that many readers won't have: if ochric epipedons and Xeric Kanhaplohumults are part of your parlance you'll cruise right through, but otherwise Chapters 5 and 6 will be a slow (if informative) read. Chapters 7 and 8 are better written and more to the point. Chapter 7 deals with animal, fungi, and microorganisms and provides the best review of serpentine-animal relationships that I have seen; the information on serpentine mycorrhizae is also well-aimed, although it lacks reference to many recent studies from Portugal and Spain, other Mediterranean-climate areas with clear applications to the California situation. Chapter 8—*Serpentine Soils as Media for Plant Growth*—is also very good and covers soil water and soil fertility in (sometimes overly) great detail.

For me, Part III—*Plant Life on Serpentine*—is the best written and best organized part of the book, especially in its treatment of individual plant responses (Chapter 9). It begins with well-done sections on ecological reasons for tolerance and intolerance to serpentine, and then (too) briefly treats evolution of serpentine endemism. This is one area where I would have liked more elaboration—a lot of interesting and important research has used serpentine as a model system to study basic evolutionary processes, and Alexander et al.'s short treatment does not do the topic justice. Chapter 10 presents a succinct overview of plant community ecology on serpentine, providing a nice outline of what we know about biotic and abiotic drivers of vegetation patterns

on ultramafics. Part III finishes with two chapters providing (Chapter 11) an overview of the basic physiognomic types one encounters on serpentine (a minor peeve: a number of species are incorrectly identified in this chapter as serpentine endemics, including *Aspidotis densa*, *Hesperevax sparsiflora*, and *Castilleja minor*), and (Chapter 12) a 46 page summary of the vegetation Alliances thus far "recognized" on serpentine soils in the western US. The Alliances are described using the American ("Daubenmire") method, which relies heavily on canopy dominants rather than considering all species in its classification. Perhaps unavoidably, Chapter 12 reads a bit like a laundry list, but it is certainly useful information.

Part IV—*Serpentine Domains of Western North* America—is the longest in the book (153 pages), and leads the reader on a virtual fieldtrip along the West Coast, beginning in Baja California and finishing in northern Alaska, providing background on geology, soils and vegetation for a total of 112 different serpentine sites. Coverage of the sites is uneven, but at any level this is a stupendous compilation of information and would have been worth publishing in its own right. The book finishes with a short Part V, which outlines land use and human health concerns associated with serpentine, and then concludes with a final "synthesis" chapter.

Overall, *Serpentine Geoecology of Western North America* is in a class by itself, as no other book treats this multifaceted topic in this kind of detail. I have a few general complaints: for example, the glossary should be expanded and glossary words in the text should be identified in bold type, and the book could have been molded into a more balanced, "cleaner" read by stronger editing (and internal inconsistencies—which are common in tomes written by multiple experts—could have been avoided). These issues don't detract from the value of the book however, and—the price notwithstanding—anyone with a serious interest in the geology, soils, and vegetation of serpentine will want *Serpentine Geoecology of Western North America* on their shelf.

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REVIEW

Ecology and Management of Giant Hogweed (Heracleum mantegazzianum). Edited by Petr Pyšek, Matthew J. W. Cock, Wolfgang Nentwig, and Hans Peter Ravn. 2007. CABI International, Cambridge, MA. 324 pp. Hard cover \$120.00. ISBN 978-1-84593-206-0.

Heracleum mantegazzianum Sommier & Levier (Apiaceae) is an unusually large invasive herbaceous species, able to grow up to 5 m tall, with 1-m compound leaves and 50–150 rays of umbels per peduncle. Besides their obvious competitiveness, plants of this species contain furanocoumarins that make the human skin vulnerable to severe sunburn. The species, native to the Caucasus Mountains, has spread across Europe creating serious environmental and health problems. It has been reported as established in at least 10 of the U.S. states. So far, it is not established in California, but it is naturalized in Oregon, Washington and British Columbia (Boersma et al. 2006; Page et al. 2006).

This volume represents the output of a three-year European Union project involving almost 40 European experts. It is an authoritative compendium of current knowledge of Giant Hogweed taxonomy, biogeography, toxicity, genetics, reproduction, seed biology, population ecology, and invasion dynamics. The possibilities of mechanical, chemical, and biological control as well as model-assisted evaluations of control strategies are also summarized in separate chapters. There are only a very few invasive plant species to whom such well elaborated monographs have been dedicated. Because this species is becoming a serious problem in several U.S. states, knowledge concentrated in this volume will be invaluable. While many infestations in the United States are still rather small, we should learn from this volume that *H. mantegazzianum* exhibited in Europe a distinct lag phase of 60 to 70 yr. The following exponential phase of spread was associated with distinct broadening of habitat preferences. Watercourses and other riparian environments were initially the major dispersal routes, but once the species started to spread beyond the river corridors, other linear habitats such as roads and railways became important. Subsequently, the species became less confined to higher altitudes and invaded warmer areas.

We may expect that several studies presented in this book will stand as model cases in plant invasion ecology and management. Petr Pyšek and his coworkers should be congratulated on this remarkable monograph on this spectacular but pernicious species!

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NOTEWORTHY COLLECTIONS

ARIZONA

ASCLEPIAS OENOTHEROIDES Cham. & Schlecht. (APOCYNACEAE: ASCLEPIADOIDEAE).—Cochise Co.: north of Portal along Noland Rd., ~100 meters north of mile marker 9, San Simon River Valley, east drainage from Chiricahua Mountains, 32°3.137′N, 109°10.882′W, 1329 m/4360 ft, 15 Sep 2003, *McGill 7399* (ASU); southeast of Portal along Portal Rd., ~50 meters northeast of intersection with Sanford Rd., 31°52.97′N, 109°4.15′W, 1295 m/4250 ft, 27 Aug 2006, *Kline 3274* (ARIZ).

Previous knowledge. *Asclepias oenotheroides* is known from adjacent Hidalgo and Grant Counties, New Mexico, but has not been recognized in the Arizona flora until now.

Significance. These collections represent a new state record for Arizona. *A. oenotheroides* (hierba de zizotes, zizotes milkweed) is superficially similar to *A. nyctaginifolia* A. Gray and a recent examination of *Asclepias* specimens (by J. Riser) at ASU reveled that a 2003 collection (*McGill 7399*) originally determined as *A. nyctaginifolia* is actually *A. oenotheroides*—the first record of this species in Arizona. *A. oenotheroides* has since been found (by C. Kline; *Kline 3274*) at another nearby location. While *A. nyctaginifolia* and *A. oenotheroides* are similar, the two species are distinguishable by *A. oenotheroides* having corona hoods approximately twice as long as the anther head and conspicuously tapering towards the base while the corona hoods are approximately three times as long as the anther head and do not taper towards their base in *A. nyctaginifolia* (R. E. Woodson, 1954, The North American species of *Asclepias* L., Annals of the Missouri Botanical Garden 41:1–211). The flowers of *A. oenotheroides* are rather gracile and greenish white to pale yellow while *A. nyctaginifolia* has more robust flowers that are white to greenish white, often with a purple tinge. At this time, *A. oenotheroides* is known in Arizona only from Cochise County, but should also be sought in eastern Graham County.

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ARIZONA

ENNEAPOGON CENCHROIDES (Licht.) C.E. Hubb. (POACEAE).—Santa Rita Experimental Range, Pasture 2SW, 200 m northwest of Rodent Station livestock exclosure, 31°49′N, 110°53′W, elev. 1150 m, 28 September 2006, *Mitchel P. McClaran and Aleta M. Nafus 06-01* (ARIZ).

Previous knowledge. Native to Africa, Arabia, Asia and India, and recently arrived, by unknown mode, in southern Arizona (Reeder, 2003, In: Barkworth (ed.), Flora of North America, Volume 25, p. 287). Previously collected from four southern Arizona mountain ranges: Santa Catalina Mountains since 1976 (*E. Schmutz s.n.* ARIZ 201849), Tucson Mountains since 1989 (*P.D. Jenkins 89-70* ARIZ), Galiuro Mountains in 2000 (*Dana Backer s.n.* ARIZ 354401), and Whitlock Mountains in 2002 (*Michael Chamberland 2013* ARIZ).

Significance. First record of this non-native, annual species on 21,500 ha Santa Rita Experimental Range, where 468 vascular species have been reported since its establishment in 1902 (Medina, 2003, In: McClaran et al. (eds.), Santa Rita Experimental Range: 100 yr (1903 to 2003) of Accomplishments and Contributions, USDA Forest Service RMRS-P-30, p. 141.). We discovered 49 *E. cenchroides* plants within 15 m radius, in a 30 ha area where numerous scientific teams have been measuring grass-mesquite relationships since 2002. Plants were found in a mesquite-grassland vegetation type that included native species *Digitaria californica* (Benth.) Henr., *Ferocactus wislizeni* (Engelm.) Britt. & Rose, *Heteropogon contortus* (L.) Beauv. Ex Roemer & J.A. Schultes, *Kallstroemia grandiflora* Torr. ex A. Gray, *Muhlenbergia porteri* Scribn. ex Beal, and *Prosopis velutina* Woot., and long (>40 y) established non-native species *Eragrostis curvula* (Shrad.) Nees and *E. lehmanniana* Nees. The discovery in 2006 may be related to wet summer conditions following a very dry winter because the species is known to increase during wet summers following severe drought in South Africa (Fynn and O'Connor 2000. J. Appl. Ecol. 37:491). In our area, precipitation at the nearby (<400 m distant) Rodent Station rain gage in summer (June–September) 2006 was 284 mm and only 36 mm in winter (October–May) 2005–2006, which are 136% and 24% of the respective averages since 1922 (McClaran et al., 2002, Santa Rita Experimental Range Digital Database User's Guide, USDA Forest Service RMRS-GTR-100, 13 p.).

All plants were carefully removed in plastic bags to limit further spread because its anemochorous dispersal can be >13 m in a 10 m s^{-1} wind (Ernst et al. 1992. Plant Ecology 102:1.) and its ability to grow in both open grassland and under tree canopy (Smit, 2005, BMC Ecology 5:4) are traits conducive to its spread and establishment in this location (Baker, 1965, In: Baker and Stebbins (eds.). The Genetics of Colonizing Species, Academic Press, New York.). Observations of its rapid spread following arrival in other southern Arizona locations (pers. comm., P. Jenkens, ARIZ), warranted our extermination effort, and continued diligence in future summers.

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CALIFORNIA

PSOROTHAMNUS FREMONTII var. *ATTENUATUS* Barneby (FABACEAE).—San Bernardino County,

California, The Whipple Mountains along the Heritage Road at 34°19.4′N and 114°34.8′W, elevation 500 m; ca. 20 plants growing in four parallel washes on a moderately steep slope near *Ambrosia dumosa*, *Larrea tridentata*, *Eriogonum inflatum* and *Opuntia bigelovii*; *J. D. Adams* (RSA) 9 May 2006. The specimens collected each contained stems, leaves and seed pods. A photograph of a seed pod was submitted to www.calphotos.berkeley.edu.

The seed pods of these plants were covered with sticky exudate that smelled like pine and tar. The clear exudate was amber on older seed pods. There were no glands visible on the seed pods. The seed pods formed after the flowers fell from the racemes. The seed pods formed about 2–3 weeks earlier than *P. fremontii* plants near the Death Valley and Providence Mountains.

These plants had considerable variability in leaf size, ranging from 1 to 3 mm wide and 6 to 15 mm long. The leaves were narrow, such as 3 mm wide by 15 mm long or 1 mm wide by 6 mm long. The plant was found to grow as a bush about 1 m high. The leaves were silvery strigose in many plants. The flowers were purple with red or green calyces.

Previous knowledge. Herbarium specimens labeled as *Psorothamnus fremontii* var. *attenuatus* have been collected from several California locations, but all of these specimens lack seed pods, which are necessary for identification of the variety (Adams and York, 2005, Madrono 52:258–61).

Significance. Because herbarium specimens of previous collections of *Psorothamnus fremontii* lack the seed pods that are necessary for identification, these are the first collections in California that include seed pods and thus can be assigned to *Psorothamnus fremontii* var. *attenuatus*; as a result, these collections extend the documented range of this variety into California.

The author is grateful to Sarah Degroot of the Rancho Santa Ana Botanic Garden, Claremont, CA for supplying map coordinates of the plants examined in this study.

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California

Astragalus kentrophyta var. *ungulatus* M.E. Jones (Fabaceae).—Mono Co., Mono Valley, 0.65 road miles E of state line on highway 167 to Hawthorne, then 2.0 road miles S on E fork of a pole line road, T3N, R29E, S10, 7050 ft. Growing with *Juniperus, Artemisia tridentata* on light-colored clay outcrops, plants prostrate, 6 Jun 1998, Arnold Tiehm 12580 (CAS, NY, RENO).

Previous knowledge. Known from Elko, Eureka, Humboldt, Lander, northern Nye, Washoe, and White Pine counties, Nevada (R.C. Barneby 1989. Fabaceae in A. Cronquist et al. Intermountain Flora 3 part B: 1-279. New York Botanical Garden Bronx, NY and recent collections).

Significance. First record for California and a range extension of about 190 km southwest. Plants were also found in adjacent Mineral Co., Nevada (Tiehm 14987 NMC, RENO).

Berteroa incana L. (BRASSICACEAE).—Lassen Co., Long Valley, Anderson (Saralegui) Ranch, 2.2 road miles W of highway 395 on highway 70 then 5.5 road miles N on Scott Road, ca. 4900 ft., 39 ° 51′19.3″N, 120 ° 05′41.6″W, WGS-1984. Growing at the edge of dry meadows, plants erect, white flowered, 14 Jul 2005, Arnold Tiehm 15023 (CAS, NY, OSC, RENO, UC, UNLV, WTU and 34 sheets distributed from NY).

Previous knowledge. "…mostly in the northern and central states from Maine to Nevada and Oregon; in Canada from Gaspé and Nova Scotia and to British Columbia (R.C. Rollins. 1993. The Cruciferae of continental North America. Stanford University Press, Stanford, CA.).

Significance. First report for California.

Physaria ludoviciana (Nutt.) O'Kane & Al-Shehbaz (BRASSICACEAE).—Mono Co., Anchorite Hills, 3.3 road miles ENE of state line on highway 359 from Hawthorne, then 3.6 road miles SW on dirt road, T3N, R29E, S 3,9. 7060 ft., 38°08′13.8″N, 118°46′19.7″W, WGS-1984, growing with *Artemisia tridentata* in areas of compacted silty sand. 26 May 2004, Arnold Tiehm 14462 with Jan Nachlinger (CAS, ISTC, NY, OSC, RENO, UC, UNLV, WTU); 15 Jun 2005, Arnold Tiehm 14986 (CAS, ISTC, NY, OSC, RENO, UC, UNLV, WTU), both collections determined by S. O'Kane, 1-2007.

Previous knowledge. Widespread from Manitoba and Minnesota, south and west to Utah, Eureka and Nye counties, Nevada, and Navajo County, Arizona (Holmgren, N.H. 2005. Brassicaceae pp. 174-419 in N.H. Holmgren, P.K. Holmgren & A. Cronquist. Intermountain Flora: Vascular Plants of the Intermountain West, U.S.A. 2 part B: 1-488. New York Botanical Garden, Bronx, NY.).

Significance. New to California and a range extension of about 240 km SW from Eureka County, Nevada. Searches in adjacent Mineral County, Nevada have been unsuccessful.

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Nevada

Polygala macradenia Gray var. *macradenia* (POLYGALACEAE).—Clark Co., Ash Creek, Red Rock Canyon National Conservation Area, Spring Mountains, in desert shrub habitat. In sandstone and limestone mixed soils with sandstone outcrops. Associated species: *Krameria erecta, Thymophylla acerosa, Coleogyne ramosissima, Eriogonum fasciculatum* var. *polifolium*, and *Ambrosia dumosa*. UTM 11s 0641228E 4002487N NAD27, 1164 m, 17 April 2006, *Trent M. Draper 58843* (UNLV).

Previous knowledge. This taxon is known to occur in Arizona, New Mexico, Texas and northern Mexico.

Significance. This is the first collection from Nevada and the Mojave Desert. Herbarium records indicate that the closest known population is 150 km to the east in the Hualapai Indian Reservation, Grand Canyon, Mohave County, Arizona. This subshrub, with its diminutive stature and with an appearance similar to that of a small *Coleogyne ramosissima*, can be easily

overlooked. It was not included in Leary and Niles' flora of the area (Leary, P. J. and W. E. Niles. 1996. *Flora of the Red Rock Canyon National Conservation Area*. Unpublished. Community College of Southern Nevada, North Las Vegas, NV). The population is within the protected boundaries (but close to inholdings) of Red Rock Canyon National Conservation Area and is therefore protected from urban encroachment.

AMBROSIA CONFERTIFLORA DC. (ASTERACEAE).—Clark Co., Cold Creek Canyon, Spring Mountains, forming large colonies in a post-fire (burned in 2000) chaparral community, on disturbed limestone soil. Associated species: *Gutierrezia sarothrae, Prunus fasciculata* var. *fasciculata* and *Ceanothus greggii* var. *vestitus*. UTM 11s 0613091E 4029844N NAD27, 1958 m, 6 September 2006, *Trent M. Draper 58839* (UNLV).

Previous knowledge. Ambrosia confertiflora occurs throughout the southern portion of the western United States, eastward to Tennessee, and into Mexico.

Significance. This is the first collection of this species from Nevada and one of the few populations known from the Mojave Desert. (It has previously been reported from the Beaver Dam Mountains, southwest Washington Co., UT [Welsh, S. L., N. D. Atwood, S. Goodrich, and L. C. Higgins. 2003. *A Utah Flora*. Brigham Young University, Provo, UT].)

SANVITALIA ABERTII GRAY (ASTERACEAE).—Clark Co., Cold Creek Canyon, just north of "Sawmill Spring," Spring Mountains, in a post-fire (burned in 2000) chaparral community, in disturbed limestone soil. Associated species: *Gutierrezia sarothrae, Ceanothus greggii* var. *vestitus, Sphaeralcea grossulariifolia, Brickellia oblongifolia* var. *linifolia* and *Hedeoma nana* ssp. *californica*. UTM 11s 0611895E 4029180N NAD27, 2119 m, 4 August 2006, *Trent M. Draper 58837* (UNLV). Specimen determined by W. E. Niles.

Previous knowledge. This taxon was collected once in Las Vegas Wash by National Park Service personnel and identified by W. E. Niles, but no voucher or other documentation was made. The species occurs in California, Arizona, New Mexico, Texas, and Mexico (J. L. Strother. 2006. *In* Flora of North America Editorial Committee, eds., *Flora of North America* 21:1–616. Magnoliophyta: Asteridae, part 8: Asteraceae, part 3. Oxford University Press, New York, NY).

Significance. This is the first collection formally documented from Nevada. The flora of the Spring Mountains is mostly well known, but the area around "Sawmill Spring" has been overlooked, probably due to the presence of nearby private land and the lack of a recognized place name on official maps. "Sawmill Spring" is named for an aging large iron boiler, fly wheels, and pieces of railroad tracks that were used in the operation of a sawmill. The author has collected 11 new Spring Mountains, county, and state records from the area.

GLYCERIA DECLINATA Breb. (POACEAE).—Clark Co., Cold Creek Canyon, "Sawmill Spring," Spring Mountains, in a post-fire (burned in 2000) fresh water riparian area. In moist dark soil derived from limestone parent material, disturbed by grazing and trampling of elk and feral horses. Associated species: *Juncus longistylis, J. ensifolius* var. *montanus, Schedonorus arundinaceus*, and *Poa pratensis*. UTM 11s 611935E 4029053N NAD27, 2128 m, 6 February 2006, *Trent M. Draper 58596* (UNLV).

Previous knowledge. This European native occurs in northeastern Nevada, California, Oregon, Arizona, Louisiana, and southern British Columbia, Canada (M.E. Barkworth and L.K. Anderson, Grass Manual on the Web at http://herbarium.usu.edu/webmanual/default.htm). In Nevada, the species has only previously been found near Lee, in Elko County.

Significance. This is only the second locality collection from Nevada. The Elko County population (approximately 400 km to the north) was discovered by A.H. Holmgren in 1941. It was treated as *G. occidentalis* in *Intermountain Flora* (Cronquist, A., A. H. Holmgren, N. H. Holmgren, J. L. Reveal, and P. K. Holmgren. 1977. *Intermountain Flora: vascular plants of the intermountain west, USA*. 6: 1–584. Columbia University Press, New York, NY.). The newest generic treatment for the Flora of North America (M. E. Barkworth and L. K. Anderson, Grass Manual on the Web at http://herbarium.usu.edu/webmanual/default.htm) recognizes the Elko County collection as *G. declinata*. The Spring Mountains material may have been introduced in hay fed to feral horses when the area was covered by snow, or from activity associated with a nearby sawmill operation.

ALOPECURUS GENICULATUS L. (POACEAE).—Clark Co., Cold Creek Canyon, along a creek fed from "Sawmill Spring," Spring Mountains, in moist limestone derived soil, heavily utilized and disturbed by elk and feral horses. Associated species: *Quercus gambelii, Rosa woodsii* var. *ultramontana*, and *Poa compressa*. UTM 11s 611935E 4029053N NAD27, 2128 m, 4 August 2005, *Trent M. Draper 57821* (UNLV).

Previous knowledge. Alopecurus geniculatus is native to Eurasia and parts of North America (W. J. Crins, Grass Manual on the Web http://herbarium.usu.edu/webmanual/default.htm). Whether the Spring Mountains population is native is uncertain. There are several records of its occurrence in northwest Nevada.

Significance. This is the first collection from Clark County, Nevada. A search of herbarium records in California, Arizona, and Utah indicate that this is the first collection from the Mojave Desert.

CARDUUS NUTANS L. (ASTERACEAE).—Clark Co., Cold Creek Canyon, along a creek fed from "Sawmill Spring," Spring Mountains, several plants in moist limestone derived soil, heavily utilized by elk and feral horses. Associated species: *Gutierrezia sarothrae, Oenothera elata* ssp. *hirsutissima, Bromus inermis, Melilotus officinalis*, and *Artemisia tridentata*. UTM 11s 611935E 4029053N NAD27, 2128 m, 4 August 2006, *Trent M. Draper 58832* (UNLV).

Previous knowledge. Carduus nutans is native to Europe and western Asia. This exotic occurs throughout much of the United States and is classified as a noxious weed in Nevada and many other states.

Significance. This is the first collection from Clark County, Nevada and one of few from the Mojave Desert. It may have been introduced in hay fed to feral horses when the area was covered by snow. Because of its invasive potential, all plants were collected and removed from the site.

I would like to thank Wesley E. Niles for his help with distribution records and reviewing the manuscript.

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NEVADA

AEGILOPS TRIUNCIALIS L. (Poaceae).—Washoe Co., Peavine Mountain, 1.1 road miles NW of Forest Boundary at end of Hoge Road on E side of mountain, T20N, R19E, S21, 5600 ft. Growing in an old burn area, abundant, 30 May 2002, Arnold Tiehm 13899 with John Korfmacher (CAS, NY, OSC, RENO, UNLV, WTU and 35 sheets distributed from NY).

Previous Knowledge. Known from California and Oregon [see herbarium.usu.edu/webmanual].

Significance. First record for Nevada (see Nevada Native Plant Society [NNPS] newsletter 28(7): 6–7. 2002).

ANEMONE DRUMMONDII S. WATSON VAR. *DRUMMONDII* (Ranunculaceae).—Washoe Co., Sierra Nevada, Carson Range, unnamed small peak NE of Mud Lake, just off trail to Rose Knob Peak, T17N, R18E, S34, 9650 ft., 39°17′43.8″N, 119°57′01.4″W, WGS-1984, growing on steep E facing, rocky, gravelly, clayey slopes, forming clumps, flowers creamy white, 20 Jul 2005, Arnold Tiehm 15024 with Jan Nachlinger (CAS, NY, OSC, RENO, UNLV, WTU and six sheets distributed from NY).

Previous Knowledge. Known from British Columbia, Washington, Idaho, Oregon, California and in Asia (B.E. Dutton et al. 1997. *Anemone* in Flora of North America Editorial Committee 3: 139–158).

Significance. First record for Nevada. Known from as close as the west side of Lake Tahoe (G.L. Smith. 1973. A flora of the Tahoe Basin and neighboring areas. Wasmann J. Biol. 31: 1–231).

CAREX VULPINOIDEA Michaux (Cyperaceae).—Churchill Co., Lahontan Valley, Fallon, 1 road mile W of Downs Lane on Reservoir Road, T19N, R29E, S28, 3945 ft., growing on the banks of the S- Canal, forming clumps to 0.7 m tall, 29 May 2003, Arnold Tiehm 14217 (CAS, NY, OSC, RENO, UNLV, WTU and 22 sheets distributed from NY).

Previous Knowledge. Widespread in Canada, US, and Mexico. In the western US known from all states except Montana, Nevada, and Utah (L.A. Standley. 2002. *Carex* section *Multiflorae* in Flora of North America Editorial Committee 23: 281–285).

Significance. First record for Nevada (see NNPS newsletter 29[7]: 5–6. 2003).

CRYPTANTHA COMPACTA Higgins (BORAGINACEAE) [*C. OCHROLEUCA* Higgins].—Elko Co., Badlands, 5.5 road miles W of road to Ferber Wash on the main road to Antelope Valley, T26N, R70E, S7, 5580 ft., growing with *Juniperus*, *Artemisia pygmaea* on gullied, light-colored clay hills, forming clumps. 10 Jun 2002, Arnold Tiehm 13989 with Jan Nachlinger (CAS, NY, OSC, RENO, UNLV, WTU).

Previous Knowledge. Known from Beaver, Garfield, Juab, Millard, San Pete, Sevier, and Tooele counties Utah (A. Cronquist. 1984. *Cryptantha* in A. Cronquist et al. Intermountain Flora 4: 223–268. New York Botanical Garden Bronx, NY; S.L. Welsh et al. 1993. A Utah Flora, 2nd ed. Brigham Young University, Provo, UT.).

Significance. First report for Nevada and a west-northwest range extension of about 81 km from Juab County, Utah (B.J. Albee et al. 1988. Atlas of the vascular plants of Utah. Occas. Pap. Utah Mus. Nat. Hist. 7: 1–670 and see earth.gis.usu.edu/plants/index.html).

CRYPTANTHA FLACCIDA (Dougl.) E.L. Greene (BORAGINACEAE).—Washoe Co., 8.5 mi NE of Red Rock, 5000 ft. Juniper, sage, 22 Jun 1938, Dan Tillotson 206 (UC); Dogskin Mountain, 3.4 road miles W of Winnemucca Ranch Road on North Fork Dry Valley Creek Road, NW end of the mountain, T24N, R19E, S6, 4820 ft., growing with *Juniperus* on rocky, silty flats. 30 May 2002, Arnold Tiehm 13893 (CAS, NY, OSC, RENO, UNLV, WTU and 30 duplicates distributed from NY).

Previous Knowledge. Known from "c. and se. Wash. to s. Calif., e. to the w. part of the Snake River Plains in Idaho (Owyhee, Ada, Boise, and Elmore cos.)" (A. Cronquist. 1984. *Cryptantha* in A. Cronquist et al. Intermountain Flora 4: 223–268. New York Botanical Garden Bronx, NY.).

Significance. First report for Nevada and a westward range extension of over 81 km from the nearest known populations in Indian Valley, Plumas County, California (see NNPS newsletter 29[4]: 3).

EUCLIDIUM SYRIACUM (L.) R. Br. (BRASSICACEAE).—Nye Co., White River Valley, White River Campground, T6N, R61E, S9, 38°23′17.4″N, 115°08′03.0″W, 5180 ft., growing in disturbed areas in the campground, 1 Jun 2005, Arnold Tiehm 14935 (CAS, NY, OSC, RENO, UNLV, WTU and 7 sheets distributed from NY).

Previous knowledge. "Established sporadically in w. U.S.; in our range [Intermountain Flora range] in c. and n. Utah" (N.H. Holmgren. 2005. Brassicaceae in N.H. Holmgren et al. Intermountain Flora. 2 part B: 174–419. New York Botanical Garden, Bronx, NY.).

Significance. First record for Nevada (see NNPS newsletter 31[8]: 6–7. 2005).

EUPHORBIA PEPLUS L. (EUPHORBIACEAE).—Washoe Co., Reno, Idlewild Park off of Booth Street, at the northwest end of the west pond, T19N, R19E, S10, 39°31′21.0″N, 119°49′57.4″W, ca. 4500 ft., growing as a weed along the railroad tracks, erect annual, 18 Oct 2005, Arnold Tiehm 15107 (CAS, NY, OSC, RENO, UNLV, WTU and 36 sheets distributed from NY).

Previous knowledge. In the western U.S. it is known from at least California, Oregon, and Utah (A. Cronquist. 1997. Euphorbiaceae in A. Cronquist et al. Intermountain Flora. 3 part A: 260–284. New York Botanical Garden, Bronx, NY.; D.L. Koutnik. 1993. *Euphorbia*. in J.C. Hickman ed. The Jepson Manual. pp 573–576. University of California Press, Berkeley, CA.).

Significance. First record for Nevada. It has been noted in other areas around Reno.

HELMINTHOTHECA (*PICRIS*) *ECHINOIDES* (L.) Holub. (ASTERACEAE).—Washoe Co., Reno, University of Nevada, Enterprise Road just W of Children's Behavioral Sciences building, T20N, R19E, S35. 4600 ft., locally common along the road, 25 Jun 1997, Arnold Tiehm 12218 (CAS, NY, OSC, RENO).

Previous knowledge. Known from "Alta., N.B., Ont., Sask.: Ariz., Calif., Conn., D.C., Iowa, Maine, Md., Mass., Mo., Mont., N.J., N.Y., N. Dak., Ohio, Oreg., Pa., Vt., Va.; Europe; widely introduced elsewhere" (J. Strother, 2006. *Helminthotheca* in Flora of North America Editorial Committee 19: 300. Oxford University Press, New York, NY.).

Significance. First record for Nevada (see NNPS newsletter 23[8]: 5. 1997).

HYMENOXYS RICHARDSONII (Hook.) Cockerell var. RICHARDSONII (ASTERACEAE).—White Pine Co., Badlands, 3.2 road miles S and SE of the county line on main road through the Badlands, T26N, R70E, S33. 5580 ft., growing with *Juniperus, Chrysothamnus parryi* on steep, brown, clay hills, forming clumps from a branched caudex, up to 25 stems per clump, 11 Jun 2002, Arnold Tiehm 14,000 with Jan Nachlinger (CAS, NY, OSC, RENO, UNLV, WTU and 33 duplicates distributed from NY).

Previous knowledge. Known from Alberta and Saskatchewan Canada, to N. Dakota, Wyoming, Colorado, Montana, and Utah (A. Cronquist. 1994. Asteraceae in A. Cronquist et al. Intermountain Flora 5: 1–496. New York Botanical Garden Bronx, NY.; S.L. Welsh et al. 1993. A Utah Flora, 2nd ed. Brigham Young University, Provo, UT.).

Significance. First record for Nevada and a north-northwest range extension of about 130 km from Millard Co., Utah (B.J. Albee et al. 1988. Atlas of the vascular plants of Utah. Occas. Pap. Utah Mus. Nat. Hist. 7: 1–670 and see earth.gis.usu.edu/plants/index.html).

IRIS PSEUDACORUS L. (IRIDACEAE).—Washoe Co., Reno, Dry Creek just W of the old Huffaker School at 7495 S. Virginia St., T18N, R20E, S6, 4470 ft., flowers yellow, style column sometimes white, leaves to 2 in wide, forming large clumps to 5 ft. tall, 23 Jun 1997 Arnold Tiehm 12217 (CAS, NY, OSC, RENO).

Previous knowledge. In the Intermountain Region known from the lower Snake River Plains (P.K. Holmgren. 1977. Iridaceae in A. Cronquist et al. Intermountain Flora 6:538–546. Columbia University Press, New York, NY.), Utah (S.L. Welsh et al. 1993. A Utah Flora, 2nd ed. Brigham Young University, Provo, UT.), and in the western U.S. also known from California and Washington (N.C. Henderson. 2002. *Iris* in Flora of North America Editorial Committee 26: 371–395. Oxford University Press, NewYork, NY.).

Significance. First record for Nevada (see NNPS newsletter 23[7]: 2. 1997).

LYTHRUM TRIBRACTEATUM Salzm. ex Spreng. (LYTHRACEAE).—Washoe Co., Duck Flat, Duck Lake, on the W side of highway 81 between Gerlach and Cedarville, NE end of the lake, T37N, R18E, S14. 4690 ft., growing on the exposed mud flats at the edge of the lake, plants prostrate, 18 Aug 1998, Arnold Tiehm 12653 (CAS, NY, OSC, RENO, UNLV).

Previous knowledge. Known from California, Idaho, and Utah (A. Cronquist. 1997. Lythraceae pp. 167–170 in A. Cronquist et al. Intermountain Flora 3 part A:167–170. New York Botanical Garden, Bronx, NY.).

Significance. First record for Nevada (see NNPS newsletter 24[8]: 3–4. 1998)

PARTHENIUM LIGULATUM (M.E. Jones) Barneby (ASTERACEAE).—Eureka Co., Fish Creek Range, foothills on extreme E side, 4.8 road miles S of highway 50 on the Duckwater road, then 0.3 road miles W, T17N, R54E, S19. 6150 ft., growing with *Juniperus, Artemisia nova* on open gravelly brown clay hills, caespitose perennial to 2 dm across, heads sessile, 2 Jun 2001, Arnold Tiehm 13557 with Jan Nachlinger (CAS, NY, RENO, UNLV).

Previous knowledge. Known from Rio Blanco County, Colorado and from Daggett, Duchesne, Emery, Uintah, and Wayne counties, Utah (A. Cronquist. 1994. Asteraceae in A. Cronquist et al. Intermountain Flora 5: 1–496. New York Botanical Garden Bronx, NY.; S. Goodrich & E. Neese 1986. Uinta Basin Flora. USDA Forest Service; J. Strother, 2006. *Parthenium* in Flora of North America Editorial Committee 21: 20–22. Oxford University Press, New York, NY.).

Significance. First report for Nevada and a range extension of over 240 km from the Uinta Basin of northern Utah (see NNPS newsletter 28[5]: 5–6. 2002). I know of no other disjunction quite matching *Parthenium ligulatum*. The closest are: *Astragalus jejunus* S. Watson which is known from SW Wyoming, adjacent Utah and Idaho, and Elko, Nye, and White Pine Counties, Nevada (R.C. Barneby 1989. Fabaceae in A. Cronquist et al. Intermountain Flora 3 part B: 1–279. New York Botanical Garden Bronx, NY); and *Leptodactylon caespitosum* Nuttall, which is known from Nebraska, Wyoming, Utah, and Elko, Eureka, Nye, and White Pine Counties, Nevada (A. Cronquist. 1984. *Leptodactylon* in A. Cronquist et al. Intermountain Flora 4:139–142. New York Botanical Garden Bronx, NY.). Both of these have a few small geographically intermediate populations in Nevada.

PSILOCARPHUS OREGONUS Nutt. (ASTERACEAE).—Elko Co., Bull Run Mountains, 0.3 road miles W of highway 11A on the road to Bull Run Reservoir, T43N, R52E, S11. 5910 ft, growing in open dried meadow areas, 16 Jul 1984, Arnold Tiehm 9038 with Barbara Ertter (CAS, NY); Elko Co., Owyhee Desert, 1.3 road miles WNW of Butte Springs on Bob Johnson Road past Hat Peak, T46N, R49E, S11, 5155 ft., growing with *Artemisia tridentata* in dry creek beds on silty flood plains, plants abundant, 10 Jun 1999, Arnold Tiehm 12883 with Jan Nachlinger (CAS, NY, RENO); Washoe Co., Mosquito Mountains, 2.0 road miles E of the state line on road from Fee Reservoir to Crooks Lake, T45N, R18E, S16, 5750 ft., growing with *Artemisia tridentata*, along small clay soiled drainages that are wet early in the year and then dry to an impenetrable "adobe", 7 Jun 2000, Arnold Tiehm 13181 with Gary Schoolcraft (CAS, NY, RENO).

Previous knowledge. "Eastern Washington, eastern Oregon, and adjacent Idaho, west into the Klamath region of southwest Oregon, and south through California. . ." (A. Cronquist. 1994. Asteraceae in A. Cronquist et al. Intermountain Flora 5: 1–496. New York Botanical Garden Bronx, NY.).

Significance. First collections for Nevada. These are the basis for Nevada being listed in Flora North America (J.D. Morefield. 2006. *Psilocarphus* in Flora of North America Editorial Committee 19: 456–460. Oxford University Press, New York, NY.).

ROTALA RAMOSIOR (L.) Koehne (LYTHRACEAE).—Washoe Co., Pyramid Lake Indian Reservation, Truckee River just upstream from the fish

hatchery between Nixon and Wadsworth, T22N, R24E, S30, 4000 ft., growing at the edge of a drying slough along the river, rooted in the water, 28 Sep 2000, Arnold Tiehm 13414 (RENO); Washoe Co., Washoe Valley, 1.6 road miles N of Bellview Overpass on highway 395, W of highway, T16N, R19E, S11, 5000 ft., 39°16′13.9″N, 119°40′08.0″W, WGS-1984, growing at the edge of ponds, 15 Aug 2006, Arnold Tiehm 15266 (CAS, NY, OSC, RENO, UNLV, WTU and 12 sheets to be distributed from NY).

Previous knowledge. In the western U.S. known from California, Idaho, Oregon, and Washington (A. Cronquist. 1997. Lythraceae pp. 167–170 in A. Cronquist et al. Intermountain Flora 3 part A:167–170. New York Botanical Garden, Bronx, NY.; E. McClintock. 1993. Lythraceae pp. 745–746 in J.C. Hickman. The Jepson Manual. Higher plants of California. University of California Press, Berkeley, CA.).

Significance. First record for Nevada (see NNPS newsletter 32[8]: 3. 2006.

SCHEDONNARDUS PANICULATUS (Nutt.) Trel. (POACEAE).—Washoe Co., Reno, Rancho San Rafael Park on NW corner of N. Virginia and N. McCarran, S of the Basque Monument, T20N, R19E, S34, 39°33′10.5″N, 119°49′53.3″W, WGS-84, 4700 ft., growing at the edge of moist areas near meadows, forming large colonies, Arnold Tiehm 14539 (CAS, NY, OSC, RENO, UNLV, WTU).

Previous knowledge. "*Schedonnardus* in a monotypic North American genus that grows in the prairies and central plains of Canada, the United States, and northwestern Mexico. It has also been found, as a recent introduction, in California and Argentina" (N. Snow. 2003. *Schedonnardus* in Flora of North America Editorial Committee. 25: 228–230. Oxford University Press, New York, NY.).

Significance. First record for Nevada (see NNPS newsletter 30[7]: 6–7. 2004).

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OREGON

ERIOGONUM UMBELLATUM Torrey var. *glaberrimum* (Gandoger) Reveal (POLYGONACEAE).—Jackson Co., Grizzly Peak plateau at the southern edge, 42°15.94′N, 122°37.17′W, elevation 1,760 m, on thin rocky-to-lithic basaltic andesite soil, a population of about 30 plants scattered on a large herbaceous flat with *Lomatium macrocarpum, Erigeron bloomeri, Sedum oregonense, Lupinus lepidus* var. *lobbii, Lewisia nevadensis*, and *Allium siskiyouense*, first collected 1 August 2006, *J. T. Duncan*, verified by J. L. Reveal from a specimen sent to him.

Previous knowledge. Known from the Warner Mountains in Lake County, OR and Modoc County, CA, plus one nineteenth century collection reported from Klamath County, OR (J. L. Reveal, *Eriogonum*, in Flora of North America, Volume 5, p. 353, 2005); based on the Oregon Plant Atlas of the Oregon Flora Project, known from five sites in Lake County along with an unverified report of it on Steens Mountain in Harney County.

Significance. First report from Jackson County and any site west of the Cascade divide. This represents a range extension of at least 150 km west of the nearest sites reported by the Oregon Plant Atlas.

LOMATIUM HENDERSONII (Coulter & Rose) Coulter & Rose (APIACEAE).—Jackson Co., Grizzly Peak plateau along western edge, two populations ca. 0.8 km apart: 1) 42°15.64′N, 122°37.58′W, elevation 1,750 m, on thin rocky-to-lithic basaltic andesite soil, a population of around 100 plants spread over an area of more than 100 m on an open flat with *Lomatium dissectum, L. macrocarpum, L. nudicaule, L. utriculatum, Ericameria nauseosa, Eriogonum nudum* var. *oblongifolium, and Penstemon duestus*, first seen and collected (in flower) on 11 May 2000; and 2) 42°16.03′N, 122°37.52′W, elevation 1,760 m, on thin rocky basaltic andesite soil, a population of a few hundred plants spread over an area of around 200 m (north and south) on a rough rocky, flat with *Lomatium dissectum, L. macrocarpum, Pinus ponderosa, Arctostaphylos patula, Eriogonum nudum* var. *oblongifolium, E. umbellatum* var. *modocense, and Holodiscus microphyllus*, first seen and collected (in fruit) 11 June 1997 (collected in flower 18 May 2001) , *J. T. Duncan*, determined by the late S. Sundberg (OSU) 2002.

Previous knowledge. Based on the Oregon Plant Atlas of the Oregon Flora Project, known in Oregon from one site in Klamath County (southeastern part, Horsefly Valley near Lorella), several sites in Lake and Harney Counties and some additional sites farther east or north.

Significance. First report from Jackson County and any site west of the Cascade divide. This represents a range extension of ca. 140 km west of nearest known site.

LOMATIUM CANBYI (Coulter & Rose) Coulter & Rose (APIACEAE).—Jackson Co., Cascade-Siskiyou National Monument, along BLM Rd 40-3E-30.0 ca.1 km west of junction with BLM Rd 40-3E-5, 42°03.10′N, 122°30.88′W, elevation 1,680 m, in coarse gravelly soil on a south-facing slope immediately south of a large borrow pit (for quarrying the same gravel), with *Lomatium macrocarpum, Chaenactis douglasii, Crepis bakeri, Arabis oregana, Cercocarpus ledifolius, Allium siskiyouense*, and *Fritellaria glauca*, collected in flower 28 May 2000, *J. T. Duncan*, verified by the late S. Sundberg (OSU) 2002.

Previous knowledge. Based on the Oregon Plant Atlas of the Oregon Flora Project known in Oregon from the south and west sides of Summer Lake in Lake County as well as additional sites farther east in Lake County and beyond to the east or north.

Significance. First report from Jackson County and any site west of the Cascade divide. This represents a range extension of ca. 170 km west of nearest known site.

—JAMES T. DUNCAN, 692 B Street, Ashland, OR 97520-2026.

OREGON

PYRROCOMA LIATRIFORMIS Greene. (ASTERACEAE).—Wallowa Co., Precious Lands Wildlife

Management Area, northeast Oregon canyon grasslands with *Pseudoroegneria spicata*, *Festuca ovina* var. *ingrata*, *Poa sandbergii*, *Solidago salebrosa*, *Gentiana affinis*, *Balsamorhiza sagittata*, *Erigeron speciosus*, *Achillea millefolium*, and *Eriogonum compositum*, T6N, R45E, S36, SW1/4, approximately 92 plants, elev. 853 m, 30 August 2005, *A. Sondenaa 676* (SRP); T5N, R45E, S12, NW1/4, approximately 50 plants, elev. 1250 m, 4 August 2005, *B. McClarin 05-0646* (OSC); T6N, R44E, S13, NW1/4, 7 plants, elev. 1128 m, 01 September 2005, *B. McClarin*, no voucher collected due to small population size.

Previous knowledge. A Palouse Prairie endemic confined to grassy hillsides and prairies in southeast Washington and adjacent Idaho (D. Bogler, *Pyrrocoma*, pp. 413–424 *in* Flora of North America Vol. 20, Oxford University Press, New York, NY, 2006). Many populations likely extirpated by cultivation of lands for agriculture. There were 80 extant populations in Idaho and Washington as of 2005 (K. Gray, et al., Updated Palouse goldenweed (*Pyrrocoma liatriformis*) occurrences on BLM land, Craig Mountain, Idaho, Idaho Fish and Game, Boise, ID, 2005).

Significance. First report for Oregon. This species is a former federal candidate for threatened status that is currently on the U.S. Fish and Wildlife Service's Species of Concern list (M. Mancuso, Palouse goldenweed (*Haplopappus liatriformis*) monitoring at Craig Mountain - 1996 results, Idaho Fish and Game, Boise, ID, 1997). *Pyrrocoma liatriformis* is considered Threatened in Washington with a Natural Heritage rank of G2 indicating it is imperiled because of rarity or vulnerability to extinction (Washington Natural Heritage Program, Endangered, threatened and sensitive vascular plants of Washington, Department of Natural Resources, Olympia, WA, 1997). Now that this rare species has been documented for northeast Oregon grasslands, Federal land managers for the U.S. Forest Service and Bureau of Land Management should initiate surveys and consider potential impacts to this species when conducting National Environmental Policy Act (NEPA) analysis for land management activities.

The field work leading to this report was funded by the Bonneville Power Administration and a Tribal Landowner Incentive Grant from the U.S. Fish and Wildlife Service.

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TEXAS

PROBOSCIDEA SABULOSA Correll (MARTYNIACEAE).—Hudspeth Co., about 1.0 mile north of Texas highway 20 and about 0.5 mile east of Acala Road, 31°20′0.20″N, 105°54′16.4″W, 1089 m, 20 September 2006, *Gutierrez 1225*, *with Gutierrez* (ASU with photos, BRIT, CAS, DES, NMC, NY, RM, RSA, SRSC, UTEP). About 20 plants observed in the area with *Portulaca oleracea*, *Portulaca halimoides*, *Cuscuta umbellata*, *Amaranthus acanthochiton*, *Tidestromia lanuginosa*, *Proboscidea parviflora*, *Heliotropium convolvulaceum*, *Gutierrezia sarothrae*, *Pectis papposa*, *Verbesina encelioides*, *Mollugo cerviana*, *Bouteloa aristidoides*, *Bouteloua barbata*, *Munroa squarrosa*, *Psorothamnus scoparius*. Chihuahuan desert scrub in deep sand dunes dominated by *Prosopis glandulosa* var. *torreyana*, *Larrea tridentata*, and *Psorothamnus scoparius*.

Previous knowledge. The type locality is in Crane County, Texas (D. S. Correll, 1966, Some Additions to the Flora of Texas, Rhodora 68: 427–428). Subsequent collections were made in Ward and Winkler Counties, Texas, in adjacent Lea County, New Mexico, and in Socorro County in central New Mexico (P. K. Bretting, 1982, A systematic and ethnobotanical survey of *Proboscidea* and allied genera of the Martyniaceae, Ph.D. Dissertation, Indiana University). A single specimen was collected by Henrickson (*Henrickson 7497*, TEX) in northern Chihuahua approximately 50 miles from the Hudspeth County collection. All specimens were collected in habitats composed of sand dunes.

Significance. These specimens are the first documented collection from far West Texas. Additional specimens should be looked for in similar sand dune habitats of West Texas and south-central New Mexico.

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WASHINGTON

ABRONIA UMBELLATA Lam. (NYCTAGINACEAE).—Pacific Co: Willapa National Wildlife Refuge, Leadbetter Point Unit, T13N, R11W, S8, NW 1/4 of NW 1/4, USGS 7.5 min. North Cove Quad. Growing in an open sandy environment in habitat restored for Western Snowy Plover (*Charadrius alexandrinus nivosus*). The restored area (currently 26 ha) lies behind a dune east of the ocean beach, and was previously dominated by *Ammophila breviligulata* and *Ammophila arenaria*. *Ammophila* was cleared mechanically and re-growth was treated chemically; the area was also lightly covered with oyster shell from Willapa Bay to maintain open, sparsely vegetated, lightly shelled, sandy habitat for Western Snowy Plover, a federally-listed ground nesting shorebird. One plant was seen on September 5, 2006 (KB); a second plant was seen on September 12, 2006 (KB & KS), 63 m east of the first plant. Both plants were flowering and setting seed. Loose fragments of both plants were collected after elk trampled them during the discovery period (*K Sayce* WS, WTU).

Previous knowledge. The historic range of *Abronia umbellata* is from western Vancouver Island, British Columbia south along the coast to northern Baja California. In Washington, it was historically documented at four sites in Clallam and Kitsap Counties, but never in Pacific County.

Significance. In Washington, *Abronia umbellata* was previously thought to be extirpated; this is the first sighting since 1950. It is likely that *A. umbellata* historically occurred within Pacific County, but was never officially recorded. Removal of invasive *Ammophila* and leveling of dunes in the habitat restoration area allowed these plants to reestablish from seeds that

remained viable in a long-lived seed bank. Native *Abronias* are thought to prefer open sand conditions; these conditions were lost when *Ammophilas* began to dominate dunes along the southwest Washington coast some decades ago. In addition to Western Snowy Plover and *Abronia umbellata*, Streaked Horned Larks (*Eremophila alpestris strigata*) also nest in the habitat restoration area, bringing the total number of state or federally listed species present in this area of open sandy habitat to three.

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WYOMING AND COLORADO

CENTAUREA MONTANA L. (ASTERACEAE).—Wyoming, Fremont Co., Lander, directly W of the Pronghorn Lodge on the banks of the Middle Fork of the Popo Agie River at N 42.83273800 W 108.72612200; Habitat: disturbed, rocky/gravelly, 30–45% slope; Associated species: *Cynoglossum officinale*, *Euphorbia esula*, *Centaurea maculosa*, *Cirsium arvense*; surrounding overstory of cottonwood and some *Salix* spp.; elevation 5357 ft; plants appear to have escaped out of an ornamental planting and have moved down the river bank to the waters edge and downstream along the water at least 100 ft; plants appear to be producing significant numbers of seed (viability not yet checked), downstream plants probably established by seed (too far for creeping roots); S. F. Enloe & H. Enloe *s.n.*, 10 June 2006 (RM).

Previous knowledge. Though long-known to be invasive, this species is still widely cultivated in the United States, including Wyoming. In states adjacent to Wyoming it is reported to be escaped from cultivation and spreading in Bannock County, ID (Cronquist 1994, Intermountain Flora, Vol. 5, New York Botanical Garden, Bronx, NY) and Salt Lake County, UT (Welsh et al. 1993, A Utah Flora, 2nd ed., Brigham Young University, Provo, UT).

Significance. This is the first documentation of this species naturalizing in Wyoming following cultivation. Eight other species of *Centaurea* are officially listed as either noxious or declared by the State of Wyoming and this species bears guilt by association.

CHONDRILLA JUNCEA L. (ASTERACEAE).—Wyoming, Sublette Co., N side of Highway 191 between Pinedale and Jackson just past Granite Hot Springs turnoff, N 43°17.149′ W 110°32.200′, elevation 6357 ft. Roadside about 2 ft. from road below a cut bank in a mixed sagebrush, aspen, conifer community. Nearly bare ground apparently recently disturbed from work on a telephone-electrical box. Adrianne Peterson *s.n.*, 28 Aug 2006 (RM).

Previous knowledge. We know of two undocumented reports of this species being found in Wyoming previously: Medicine Lodge Creek, near Hyattville, Big Horn Co. in about 1998, and near Alpine Junction, Lincoln Co. in about 2005. This species is designated noxious by nine western states, four of these adjacent to Wyoming (USDA, NRCS. 2006-11-15. The PLANTS Database (http://plants.usda.gov). National Plant Data Center, Baton Rouge, LA). *Chondrilla juncea* is strongly favored by disturbance and is closely associated with *Bromus tectorum*, apparently following on the heels of cheatgrass infestations.

Significance. In other western states such as Idaho, this species has invaded disturbed and undisturbed plant communities and has interfered with wheat-harvesting machinery. This is the first documentation of this noxious weed in the state, and botanists should voucher and report any future Wyoming sightings to local weed control authorities to prevent costly infestations. Long term potential impacts are severe.

ECHIUM VULGARE L. (BORAGINACEAE).—Wyoming, Laramie Co., Near Cheyenne, railroad right of way embankment about 100 m South of Otto Road, N 41.09 W 105.05. Habitat: high plains grassland with *Cynoglossum officinale* and *Bromus tectorum*, elevation ca. 6100 ft. Bruce Shambaugh *s.n.*, August 2004 (RM). Wyoming, Laramie Co., near Cheyenne, Union Pacific Railroad tracks and vicinity along Otto Road, N41.09° W105.01°, elevation ca. 6700 ft.; both sides of RR track, road, and barbed wire fences; ca. 2 m stretch seen despite recent herbicide treatments; spreading away from road & railroad tracks into pastureland; Brasher, S. Franklin, & K. Nelson 3441, 10 Aug. 2006 (RM). Colorado, Grand Co., Kremmling, N 40.0601 W 106.3989, CO Highway 9 roadside on SE edge of town with *Bromus inermis*, 1 large single plant, S. F. Enloe *s.n.*, Aug 2005 (RM).

Previous knowledge. The first documentation of this species in Wyoming is Dorn 4371 (RM) in 1986, Laramie Co., near Cheyenne, followed by three other Dorn collections housed at RM (Albany & Uinta cos., 1992; Platte Co., 1993), then E. J. Hoffman *s.n.*, July 2000 in the Laramie Mountains, Laramie Co. The Kremmling, CO specimen is only the second specimen for Colorado at RM, with none being housed at COLO.

Significance. *Echium vulgare* is listed as a noxious weed in Washington. Though previously known from Colorado and Wyoming, this species was not perceived as a problematic weed requiring control efforts until the vicinity of Dorn's 1986 collection was revisited by Shambaugh. The infestation was mapped in 2004 (University of Wyoming Cooperative Agricultural Pest Survey (CAPS)http://uwadmnweb.uwyo.edu/capsweb/) and had spread to over 113 ha along an 8 km stretch of railroad tracks. Collectors should voucher and report other sightings of this weed in Wyoming and Colorado. This weed, like many other borages is poisonous to livestock due to its pyrrolizadine alkaloids, and like some other borages has long stiff hairs that cause contact dermatitis in humans.

RORIPPA AUSTRIACA (Crantz) Bess. (BRASSICACEAE).—Wyoming, Sublette Co., 2 m NE of Cora Highway on WY Highway 352 at Bootjack Ranch, N 42°58.254′ W 109°58.780′, elevation 7415 ft., just across fence from irrigated pasture, common here in the bottom of irrigation ditches. Currah *s.n.*, 1 August 2006 (RM). Sublette Co., ca. 3 m N of Cora, ca. 1 mi. E of WY Highway 352 on county road at N 42.98846 W 109.99312; ca. 7400 ft. elevation; roadside in pastureland, the infestation including cultivated fields, irrigation ditches, irrigated pasture, and roadsides, spanning

parts of multiple acres; 25 August 2006; Brasher, Enloe & Peterson 3475 (RM).

Previous knowledge. *Rorippa austriaca* is currently listed as a noxious weed in four states: Alaska, Arizona, California, and Washington. This weed is not on the Wyoming state noxious weed list, nor has it been declared in any county of Wyoming.

Significance. This is the first documentation of this noxious weed in Wyoming, and botanists should voucher and report any future Wyoming sightings to local weed control authorities to prevent costly infestations. Because this species grows in moist soil it has potential to invade ecologically important wet areas such as floodplains, and economically important agricultural lands including fields, pastures, and ditches.

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SPECIAL ISSUE

ECOLOGICAL RESTORATION IN A CHANGING WORLD: CASE STUDIES FROM CALIFORNIA

CONTENTS

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RESTORATION IN A CHANGING WORLD: CASE STUDIES FROM CALIFORNIA INTRODUCTION TO SPECIAL ISSUE

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As the human footprint occupies an ever increasing proportion of the earth's surface and resources (e.g., Vitousek 1994; Vitousek et al. 1997; Tilman et al. 2001; Wackernagel et al. 2002), conservation biologists must develop strategies that both protect remnant natural areas and rebuild the ecological integrity of highly altered landscapes (Young et al. 2005). In almost no other region on earth is this need more imperative than in California. California is home to over 36 million residents and has roughly the 7th largest economy in the world, making it a highly human-influenced environment. Yet, the state possesses an exceptional diversity of ecosystems and taxa, many of them threatened with extirpation. The California Floristic Province has been classified as a World Biodiversity Hotspot because of its exceptional level of species endemism and the conservation challenges it faces (Meyers et al. 2000; Konstant et al. 2005).

While the mission of the California Botanical Society is to advance the science of western American botany, today it is evident that a key element to that science is learning how to restore native plant communities so that native biodiversity can be sustained over time. There is still much to be learned and the science of restoration ecology is still in its infancy. Furthermore, the practice of ecological restoration must be accomplished in the face of dynamic global changes. In 2005, our board was invited to sponsor a symposium at the 2006 annual meeting of the Society for Conservation Biology (SCB) to be held in San Jose, CA in June 2006. The theme of the conference was "Conservation without Borders". This opportunity inspired us to organize the symposium "Restoration in a changing world: Case studies from California" which took place on Wednesday, June 28, 2006. This special issue is the culmination of that effort.

The symposium delivered eight 15 min papers by Michael Vasey, Stuart Weiss, Jeffrey Corbin, K. Blake Suttle, John Callaway, Nathan Stephenson, Jodi McGraw, and Alison Purcell. There was a remarkable congruence between most of these talks and, in fact, several other talks and symposia at the SCB meeting. The common theme was that the threats posed by such elements of global change as climate change (including associated sea level rise), invasion of non-native species, alteration of disturbance regimes, and the input of nitrogen via air pollution are exerting unprecedented pressure on biodiversity, trophic interactions, and the physical structure of ecosystems in California and throughout the world. As many authors have recognized, multiple components of global change are also capable of interacting with each other to affect ecological interactions and the prospects for successful restoration (e.g., Dukes and Mooney 1999; Weiss 1999; Vila et al. 2007). Although Rein et al. (this volume) did not participate in the symposium, we welcome their contribution to this special issue as yet another good example of the challenges that invasive species pose to restoration practitioners. Taken collectively, the results presented in the symposium and in this special issue suggest that the challenges that face sensitive ecosystems will be substantial and will, in some cases, require wholly new strategies if we are to successfully preserve biodiversity and ecosystem function in this age of global change.

California is hardly unique in North America, let alone worldwide, in confronting the challenges of climate change, invasive species, and changing land-use. Indeed, nearly every part of the globe must deal with one or more of them. This special issue considers the future of conservation and restoration efforts in California in the face of the myriad threats posed by the local and regional manifestations of several of the most important drivers of global change. We hope that insights gained from these papers can be helpful to scientists and habitat managers in other regions who must also confront the challenge of restoring ecosystems in the face of these challenges.

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We thank Erica Fleischman from the Society for Conservation Biology (SCB) for inviting us to participate in the annual SCB meeting in 2006. Speakers at the

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symposium (listed above) gave stimulating talks and most participated in a vigorous discussion after the symposium that included what steps restoration science should take in the future. We also appreciate the support of the board of the California Botanical Society for agreeing to sponsor this symposium and for committing to publish this special issue based on that event. The California Biodiversity Center graciously contributed funds that helped bring the speakers to the symposium. Finally, we thank *Madroño* Editor-in-Chief John Hunter for his patience and excellent support in bringing the papers to press.

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ECOLOGICAL RESTORATION IN CALIFORNIA: CHALLENGES AND PROSPECTS

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ABSTRACT

Given the rich biological diversity in California and dramatic loss and modification of its habitats, populations, species, and ecosystems, a concerted effort has emerged to restore large areas of the state's public and private lands. Under these circumstances, ecological restoration represents an important element in the strategy to conserve numerous at-risk species and maintain vital ecosystem services. After reviewing the various motivations for ecological restoration, we identify some of the key challenges, both practical and theoretical, that are likely to affect the success of restoration efforts. We describe a shift in defining restoration success from a focus on recreating historic "pristine" ecosystems to viewing restoration in a dynamic landscape context in which realistic novel ecosystems are accommodated. These accommodations are necessitated by a broad array of challenges that include several global change factors. Finally, we argue that prospects for successful ecological restoration will be enhanced by emphasizing landscape-scale resilience and incorporating restoration into a regionally-coordinated, active adaptive management program.

Key Words: adaptive management, California, ecological restoration, global change, novel ecosystems, resilience.

California is renowned for its extraordinary levels of biological diversity. The California Floristic Province has been recognized as one of 25 global biodiversity hot spots (Meyers et al. 2000; Konstant et al. 2005) with an estimated overall endemism of vertebrates and insects and other invertebrates exceeding 50% and of vascular plants approximating 35% (Schoenherr 1992). This degree of endemism is remarkable for a large continental region located in the temperate zone.

Numerous reasons have been advanced to explain this diversity (e.g., Stebbins and Major 1965; Stebbins 1978; Raven and Axelrod 1978, Davis et al. 1997). These fall into a combination of three premises: (1) California has served as a refuge for a flora and fauna that was once much more widespread over western North America during the Middle-Tertiary but that became progressively restricted in range due to cooling and drying of the interior; (2) California served as a cauldron of evolution during the Pleistocene, especially among annual plants and insects, as numerous glacial and inter-glacial cycles provoked frequent migratory shuffling of species assemblages while the advent of an extreme Mediterranean climate drove adaptation to a higher frequency and intensity fire regime; and (3) California presents a remarkably heterogeneous combination of geology, soils, hydrology, climate, and topography comprising a fine-grained substrate on which various species assemblages have been able to differentiate. The net result of this diversification is an estimated 300 natural communities, 178 habitat types (Schoenherr 1992), 10 floristic provinces, and 24 floristic sub-provinces (Hickman 1993). A key point is that change, and particularly the recent climatic changes during the Pleistocene, have been an important driver in California's biotic diversification. Change is not inherently bad, but it clearly can have important ecological and evolutionary manifestations.

Hoekstra et al. (2005) list most of the California ecoregion as critically endangered based on the extremely high habitat conversion rate relative to area protected. Noss (1994) and Noss and Peters (1995) note a range of highly threatened California ecosystems, including coastal strand and dune, southern California coastal sage scrub, large rivers, riparian forest and wetlands, native grasslands, old growth ponderosa pine forests, cave and karst systems, and ancient Pacific Northwest forests. Less than 10% of the original extent of vernal pool habitat (Zedler 2003) and about 10% of tidal wetlands (Zedler 1996) remain. More than 99% of grasslands in California are now dominated by non-native species (Davis et al. 1997). This habitat loss and transformation has led to extensive fragmentation and isolation. Non-native invasive species and various kinds of pollution add additional stresses to these habitat remnants. This combination of conditions may lead to an "extinction vortex" (Gilpin and Soulé 1986) that,

absent intervention, can progress down an irreversible path toward species extinction.

Super-imposed upon the California landscape is the influence of human populations. Beginning with the first establishment of human settlements between 12,000 and 15,000 yr ago, humans have significantly influenced the distribution and composition of communities. For example, Anderson (2007) reviewed the use of fire by Native Californians to improve hunting, provide defensible areas surrounding villages, and enhance germination of desirable species, among other reasons. Today, human populations have an even greater impact on species composition and biodiversity, as there are now approximately 36 million people in California and a growth rate of 13.6% per decade (U.S. Census Bureau 2006). Understandably, future population growth has provoked alarm at prospects for the future of biodiversity in California (e.g., Jensen et al. 1993). In particular, even at the level of popular conservation advocacy (Brower and Chapple 1995), recognition has emerged that preservation of California's remnant wild ecosystems is not enough; rather, it is considered imperative that we begin the process of restoring and reconnecting threatened habitats if we are to prevent the current and growing extinction crisis (Wilson 2002).

In this review, we explore the relationship between ecological restoration and biodiversity conservation in the future. To set the stage for this analysis, we evaluate the range of motivations and endpoints for restoration in California and elsewhere. We then illustrate a number of challenges confronting restoration efforts, focusing on issues of landscape context and global change. Finally, we review contemporary literature in restoration ecology that poses some alternative prospects for how to best adjust conservation strategies to mesh with these overarching realities. While the application of these approaches is critical to conserving biodiversity in California, they are equally compelling in a wide array of venues experiencing similar conservation challenges.

Motivations and Endpoints for Restoration

Restoration of damaged ecosystems in California and worldwide is motivated by myriad reasons (Ehrenfeld 2000; Clewell and Aronson 2006) and is undertaken by a wide array of actors, ranging from volunteer community groups focusing on small (sometimes less than one hectare) sites to large multi-public agency consortiums engaged in projects involving thousands of hectares (e.g., the South Bay Salt Pond Restoration Project along the shores of the San Francisco Bay). Often restoration is initiated to achieve specific conservation goals, such as preventing the extinction of endangered species and the habitats on which they rely (Ehrenfeld 2000). For example, restoration of dune habitat in Lobos Valley on the Presidio of San Francisco was motivated in large measure by the desire to recover a federally listed endemic annual plant species, the San Francisco Lessingia (*Lessingia germanorum*). This effort increased the number of individuals from the low hundreds to approximately one million (Albert 2001), while also restoring an ecological educational resource in the heart of San Francisco (Holloran 1998). Many restoration projects also aim to provide important ecosystem services for humans such as water treatment provided by wetlands or rehabilitation of drastically disturbed ecosystems, such as mines and areas contaminated by chemicals that may negatively affect human health. Federal and state laws (e.g., the Endangered Species Act, Section 404 of the Clean Water Act, Surface Mining and Reclamation Act) recognize these public values and mandate restoration of certain habitats or species. Clewell and Aronson (2006), however, highlight that restoration may be motivated by other reasons, such as attonement for environmental damage, reentry into nature, renewal of the nexus between nature and culture, and spiritual renewal. Indeed, many efforts to remove invasive non-native species in California are not mandated by law and are largely staffed by volunteer labor.

Our goal here is not to provide an exhaustive list of motivations for restoration, but rather to note the diversity of reasons behind restoration that will necessarily lead to differing goals of restoration projects. The increasing recognition of these different goals is reflected in the broadening definition of restoration. Early publications in the field of restoration strove to distinguish between restoration (an effort to restore 'predisturbance' conditions) and efforts that aimed to reclaim or rehabilitate certain, but not all, species and ecosystem functions (Cairns 1983; Bradshaw 1984). In contrast, the recent Society for Ecological (SER) definition of ecological restoration is much more inclusive. Ecological restoration is now defined as "intentional activity that initiates or accelerates the recovery of an ecosystem with respect to its health, integrity and sustainability" (SER 2004). This newer definition reflects the varied goals of different restoration projects, as well as the recognition that given historical contingencies and the dynamic nature of ecosystems, it is impossible to achieve a highly fixed restoration endpoint. As we argue later, changing global conditions make a broader view of the endpoint of restoration essential.

Trying to restore an exact replica of the full suite of pre-disturbance species is not the sole reason for restoration or, perhaps, the most publicly compelling. Yet, biotic diversity is likely

to benefit from ecological restoration no matter what the motive. What is essential is that the goals of each restoration project are clearly stated at the outset, and reflect a certain degree of consensus among parties involved, so that the degree of success of the restoration project can be evaluated (Ehrenfeld 2000; Holl and Cairns 2002).

Challenges for Ecological Restoration in California

Although debates about the motivations and endpoints of restoration are longstanding, increasing recognition of the temporal and spatial scale of human alteration require us to re-evaluate the goals of restoration in California and elsewhere. Here we discuss how the spatial scale that is necessary to restore ecosystem processes in the face of increasing impacts of global change will necessarily change how restoration is implemented and its success evaluated. Despite the diversity of actors and scales of projects, a common thread tying most restoration efforts together is that they are narrowly confined to a given piece of land, waterway, or particular habitat type (e.g., tidal wetlands). Although it is widely recognized that the long-term success of restoration is dependent on the landscape-matrix in which it is embedded, this recognition is rarely put into practice (Holl et al. 2003). Recent studies demonstrating the ecological importance of cross-habitat subsidies (Polis et al. 2004) have served to reinforce the key role adjacent ecosystems can play in the ecological health of target restoration habitats.

Considering restoration in a landscape context becomes particularly critical when viewed through the lens of the serious challenges to ecological restoration now represented by global change. Global change agents that may dramatically affect ecological restoration in the future include: (1) several related phenomena associated with rapid climate change including an increase in temperature, sea level rise, altered precipitation patterns, and increased extreme weather events; (2) the introduction of invasive non-native species, including disease microbes; (3) the atmospheric deposition of pollutants, e.g., nitrogen, and their influence on biogeochemical cycles; and (4) changing socio-economic patterns that affect land use practices (Vitousek 1994; MEA 2005). Many of these are discussed in more detail in other articles in this special issue of *Madroño* that is dedicated to exploring the topic of ecological restoration in a changing world using case studies from California (Suttle and Thompson 2007; Callaway et al. 2007; Purcell et al. 2007; Rein et al. 2007; all in this volume).

Climate Change. Potential developments associated with rapid climate change may represent the most important and least appreciated problem facing restoration practitioners (Harris et al. 2006). There are now clear signals that climate change is affecting a host of biotic relationships (e.g., Parmesan and Yohe 2003; Root et al. 2003; Thomas et al. 2004; Parmesan 2006). With a Mediterranean climate, California is particularly vulnerable to changes in rainfall patterns, snow pack storage, hydrology, temperature, and sea level rise (Callaway et al. 2007). Whereas past efforts to conserve and restore at-risk species have focused on a restricted set of habitats impacted by large human populations (e.g., wetlands and coastal dunes), it is now likely that some of the most at-risk species are those that inhabit a broad array of environments and, absent climate change, would be considered safely protected, such as high Sierran endemics and isolated edaphic endemics with nowhere to migrate if local climate becomes unfavorable. In this dynamic environment, active intervention and strategic ecological restoration and management may be the only possible solution for "life boating" several species through this episode of rapid climate change. It is likely that major investments in current ecological restoration projects will need to be modified to account for problems such as rapid sea level rise and other predictable climate-related phenomena, such as altered rainfall patterns. These rapid climate changes, in other words, assure that historical ecosystems will not serve as a faithful reference template for future restored habitats.

Invasive Species. The challenge of invasive species to ecological restoration is all too well known (D'Antonio and Myerson 2002; D'Antonio and Chambers 2006). It is safe to say that the vast majority of ecological restoration activities in California are beset with a suite of non-native invasive species. In an ideal world, restoration would involve stimulating ecological processes, such as fire, natural succession, and sediment deposition that would lead over time to desired natural communities. When non-native invasive species enter the system and set off in unpredictable trajectories, they act to potentially exclude desirable native species and undermine desired outcomes. Since these non-native species usually come from other Mediterranean regions (Major and Barbour 1988) they are well-suited to California's Mediterranean climate and thrive under current disturbance regimes. Further, non-native invasive diseases, such as *Phytopthera ramorum*, the agent causing Sudden Oak Death, and West Nile virus impact natural populations of common species, such as oaks and corvid birds, creating trophic impacts to various levels of species assemblages. The challenge of invasive species, like climate change, may represent a virtually intractable reality that will simply

have to be accepted and integrated into ecological restoration goals and practices (D'Antonio and Meyerson 2002; Keeley 2005). The omnipresence of invasive species may be the most powerful argument of all that there is no turning back to some vision of a "pristine" historic ecosystem in California.

Atmospheric deposition. The challenge of atmospheric nitrogen deposition is an insidious phenomenon that affects several ecosystems in California. For example, in species rich serpentine grasslands located in areas with high volumes of automobile traffic, nitrogen deposition promotes the success of non-native annual grasses that suppress native annual herbs which are utilized by rare butterflies such as the Bay Checkerspot, consequently reducing the population viability of this endangered species (Weiss 1999). In southern California, montane chaparral and yellow pine forests are impacted by the combination of both ozone and nitrogen pollution due to summer smog inversion effects (Fenn et al. 2003). While above-ground biomass increases due to a fertilization effect, below-ground fine root mass and carbohydrate allocation are decreased, resulting in heightened vulnerability of these communities to wild fire. Also, nitrate runoff is increased dramatically, causing eutrophic impacts to aquatic habitats that are influenced by this runoff. These are just a few of the manifestations of a broader problem involving the general disruption of global biogeochemical cycles due to pollution. Similar to climate change, the effects of pollution are large-scale and rapid relative to geological time. However, their presence is not directly appreciated in the typical time scale of ecological restoration planning and implementation. It is likely that disruptions of biogeochemical cycling are another major factor that is shaping ecological restoration activities in ways that are still yet poorly understood but that will increasingly influence restoration trajectories.

Land-use practices. A final element of global change that merits attention is the socio-economic drivers of land use practice (Vitousek 1994; MEA 2005). Land use practice in California is governed by a complex web of national, state, and local policies that attempt to protect the public trust (e.g., conserve natural resources) while contending with a majority of lands that are privately owned (Jantz et al. 2007). As local economies increasingly become part of a globalized market, unexpected changes in global economic conditions (e.g., new markets or lost markets) can have major impacts on local land use patterns (Lambin et al. 2001; Wadley et al. 2006). For example, a relatively sudden surge in the demand for wine can lead to large-scale loss of oak woodland and chaparral habitat on slopes surrounding California's coastal and interior valleys. Declines in prices of beef can cause ranchers to sell their ranches for suburban home development. Development of homes in flood plains in the Sacramento Valley can affect the ability to create setback levees and to restore riparian forests. All of these local and regional economic phenomena are today linked to a global economic engine that is highly dependent upon factors that transcend California's economy.

Importance of Social Context

Although it is clear that restoring ecological processes will require large-scale coordination, a major challenge is how to create institutional mechanisms that will coordinate and support restoration activities at landscape and even regional scales among a diversity of actors over extended periods of time. There are numerous examples of this sort of coordination ranging from Coordinated Resource Management and Planning groups confined to single watersheds to the CALFED Bay-Delta Authority that encompasses the entire drainages of the Sacramento and San Joaquin rivers (approximately 40% of the land area of California). A promising example is the 2003 law (SB 107) creating a California Natural Communities Conservation Program (NCCP). California's NCCP focuses on natural communities in which at-risk species are found, but it also takes a broader landscape and/or regional approach to conservation strategies. For example, a Yolo County Habitat Conservation Plan (HCP/NCCP) currently underway (2006) involves a Joint Powers Agreement between several cities and Yolo County. A recent scientific advisor's report pertaining to this Yolo HCP/NCCP (Spencer et al. 2006) outlines a series of management recommendations that involve restoration practices that are designed to improve habitats for a variety of at-risk and more common species. The virtue to such a plan, when and if adopted, is that local governments can create zoning and other land use regulations that have greater potency in guiding land use decisions and practices than virtually any other public policy mechanisms (Jantz et al. 2007).

Unfortunately, these NCCPs and HCPs generally do not go far enough to engage the broader public, including multiple restoration actors, in strategic conservation and restoration activities. Rather, there is still a perception that these conservation plans have a long way to go to reconcile the inherent conflicts between human land use practices and the preservation of biodiversity (Feldman and Jonas 2000). Also, analyses of the focus on listed species for multispecies conservation planning has come under criticism for its inadequacy (Rubinoff 2000; Rahn et al. 2006). But, the recent passage of a strengthened law and the wave of new NCCP proposals

underway may represent important forerunners of the kinds of institutions that ultimately could be applied to this need for landscape and regional coordination.

Such efforts to coordinate actions are necessary not only because of the spatial scale of such projects, but also because a reactive counter-movement has emerged that presents a considerable level of social resistance to some ecological restoration activities (Gobster 2000). This social resistance can create major roadblocks to restoration activities that impact both the cost and timeliness of restoration implementation. Social resistance can occur both in an urban context, as with the San Francisco Natural Areas Program where dog walker and tree advocate citizen groups derailed a management planning process for remnant natural areas (Garcia 2002a, b), and in rural environments, such as the ambitious Sacramento River Restoration Program where some involved farmers perceive restored areas as having negative impacts on agricultural production (Golet et al. 2006; Buckley and Haddad 2006).

Causes for social resistance to ecological restoration are multiple. However, one problem stems from a conceptual challenge to restoration ecology itself, namely, the definition of "restoration" and how practitioners and the public interpret this concept. For practitioners, there is still controversy over whether restoration should be focused on recovering ecosystems to some type of historic "pristine" reference condition or whether restoration should be viewed as a process in which future ecosystems are shaped to maximize native species persistence, ecosystem functions, and ecosystem services. For some people, the notion of moving society back towards a more "pristine" nature is a threatening prospect. Consequently, the rationale of re-creating historic natural conditions may be one of the primary deterrents to public support for restoration activity.

Given the difficulties in coordinating heterogeneous restoration activities, and the challenge of generating public support for these activities, it is vital that socio-economic investments in restoration are grounded in a robust scientific framework (Falk et al. 2006). Much of the information from various projects that could help to improve restoration science is not being gathered nor communicated (Holl et al. 2003). A major problem is the lack of investment in monitoring and adaptive management. For example, Bernhardt et al. (2005) synthesized information on 37,099 national river and stream restoration projects. Only 10% of these projects had any post-implementation assessment or monitoring. Of the approximately 3700 that did receive some post-implementation evaluation, most did not evaluate consequences of restoration activities or provide for dissemination of monitoring results. Clearly, for "adaptive management" to be meaningful, there must be at least as great an investment in "learning" as in "doing" (Vasey 2003) and a much stronger effort made to engage academic scientists, students, and restoration practitioners (e.g., agency, non-profit, and consultants) in partnerships in which these adaptive management programs are designed and implemented. Such an effort should include more funding and incentives for creating effective public outreach. Perhaps, by encouraging a more "public ecology" (Robertson and Hull 2001) in which science-based alternatives are explored in a transparent manner with public stakeholders (Purcell et al. 2007, this volume), the onus to coordinate restoration activities at broader scales in a publicly supportive environment might take root.

Efforts to promote an exchange of information and opinions among land owners, government agencies, and scientists are necessarily challenging, costly, and time consuming, but essential to the success of large-scale restoration efforts. Two good examples involve the exploration of alternative futures with stakeholders in the Willamette Valley, Oregon, where GIS tools and computer models were used to explore future land use scenarios with stakeholders in the region (Baker et al. 2003) and a similar public outreach process involving large-scale management of fire-prone ponderosa pine ecosystems and the urban-wildland interface (Sisk et al. 2006). Other well publicized large-scale collaborative institutional arrangements for conserving and restoring natural resources, such as the CALFED Bay-Delta Program and the Everglades Comprehensive Restoration Plan have met with mixed success (Heikkila and Gerlak 2005). CALFED began in 1994 as a forum for federal and state agencies to develop a plan for managing the region around the San Francisco Bay and San Joaquin-Sacramento River Delta. It now includes 23 state and federal agencies responsible for adaptively managing water resources and protecting natural resources and funds a great deal of science to inform management decisions in this region (Jacobs et al. 2003; Heikkila and Gerlak 2005). It has led to dialogue among scientists, local landowners, and many government agencies, much better coordination of management activities, and an improved transparency of science that is used for decision making. But achieving these goals has been a long and arduous process, and CALFED has been criticized for spending millions of dollars without clear evidence of accomplishments.

Prospects for the Future of Ecological Restoration in California

The new definition of ecological restoration, with its focus on the recovery of ecosystem

health, integrity and sustainability (SER 2004), helps to push the science and practice of ecological restoration beyond the goal of recreating historic ecosystems. In the future, ecosystems are more likely to be shaped so as to both perpetuate indigenous species and ecological functions while accommodating global change in a more flexible and adaptive framework. This conceptual shift in the focus of restoration ecology is gaining momentum (e.g., Aronson and van Andel 2005; Palmer et al. 2005; Hobbs et al. 2006; Harris et al. 2006). For example, Hobbs et al. (2006) explore the potential importance of "novel ecosystems" (i.e., "emerging ecosystems") that can be defined as "ecosystems containing new combinations of species that arise through human action, environmental change, and the impacts of deliberate and inadvertent introduction of species from other regions". Palmer et al. (2005) highlight the importance of selecting a "guiding image" for river restoration that is a realistic approximation of an achievable result: "Rather than attempt to recreate unachievable or even unknown historical conditions, we argue for a more pragmatic approach in which the restoration goal should be to move the river towards the least degraded and most ecologically dynamic state possible, given the regional context" (p. 210 in Palmer et al. 2005).

It is noteworthy that some of the most advanced thinking along these lines comes out of Europe, a region in which landscapes have been transformed by human practices for many millennia. Folke et al. (2002) and Bengtsson et al. (2003) articulate the need to tailor conservation practices to enhance resilience, defined as the "capacity to buffer change, learn and develop", and the importance of adaptation to dynamic human-influenced landscapes. Recognizing the likely influence of global change, Bengtsson et al. (2003) advocate a landscape-scale approach to preserving "ecological memory"; i.e., the species, interactions, and structures that make ecosystem reorganization possible in the face of changed conditions. Similar calls come from the contemporary American environmental movement, such as David Brower, who pointed out that "Restoration is not an effort to stop the clock, but rather a chance to keep the clock running—in fact, our best chance" (p. 99 in Brower and Chapple 1995). Brower envisioned a combination of Conservation, Preservation, and Restoration (CPR)—a metaphor for earth resuscitation—as the key strategy for recovering the earth's ecological vitality.

Given the challenges in which ecological restoration and conservation management are being practiced today in California and elsewhere, we believe that it is critical that we embrace the creative potential inherent in this more adaptive focus on shaping future ecosystems. However, moving from a general call for a broader view of restoration endpoints to making specific recommendations for how to design restoration plans in light of climate change is challenging, particularly given the uncertainty in the models that make specific predictions about how climate change will be manifested (Weltzin et al. 2003; Callaway et al. 2007). Many have suggested increasing habitat connectivity in fragmented landscapes to allow for species migration in response to a changing climate (e.g., Donald and Evans 2006; Wilmers and Getz 2005) demonstrate the importance of restoring intact food chains to buffer changing climatic conditions. Other authors have noted the need to consider whether there is sufficient genetic variation in the propagules introduced as part of restoration to allow them to adapt to and survive in future climate conditions (Rice and Emery 2003; Sáenz-Romero et al. 2006). Increasingly, there is recognition that wetland restoration projects need to be designed recognizing predicted sea level rises, although the specifics of the rate of rise are difficult to predict (Georgiou et al. 2005; Callaway et al. 2007). How to design restoration for future conditions will certainly be a growing area of research, but will necessarily remain challenging given the uncertainty regarding the many climatic feedbacks and other global changes at play (Rein et al. 2007; Suttle and Thomsen 2007; Callaway et al. 2007; all in this volume).

This broader view of restoration is likely to be more inclusive of different stakeholder's needs and, therefore, should find broader public support than a simple focus on restoring a few endangered species. But, broadening the definition of restoration potentially increases the conflicts about restoration goals and endpoints. As we have noted earlier, the primary challenges to managing in a landscape context are as much social as biological in that they involve policy coordination, overcoming social resistance, and supporting a more actively engaged scientific community in the practice of restoration ecology (Holl et al. 2003). Resolving conflicting needs will require embracing the recent movement towards stakeholder participation throughout the restoration planning, implementation, monitoring, and adaptive management process (Holl and Cairns 2002; Palmer et al. 2005). As discussed previously, this is a long and challenging process, but engaging in this dialogue from the outset is much more likely to result in success in the long run (Palmer et al. 2005).

Ultimately, the key to our ecological and evolutionary future is promoting resilience and adaptation to what are likely to become increasingly dynamic landscape processes (Folke et al. 2002; Bengtsson et al. 2003; Carpenter and

Folke 2006). Under this scenario, it is probable that ecological restoration will play an increasingly important role in shaping the future of California's ecosystems and in creating a bridge for its rich biological diversity to survive these changes as California's ecosystems experience biological reorganization. It behooves the ecological restoration community to adjust to this new reality by adopting realistic standards for restoration (Palmer et al. 2005). Also, it is essential to frame future restoration projects in a landscape context and to account for the emergence of novel ecosystems. Finally, there must be greater investment in not only doing but *learning* as well; i.e., the practice of developing robust scientific approaches to conducting active adaptive management. This will require the support of the public, government, and the scientific community—a tall order but a necessary one if the practice of ecological restoration is to be a cornerstone in sustaining California's biodiversity and its future ecological health.

Summary

Ecological restoration will be a key to conserving California's rich biodiversity, however, the future impacts and uncertainties inherent in global change require that we adjust our approach to the science and practice of restoration ecology. In particular, we need to embrace a broader definition of restoration ecology that focuses more on shaping future ecosystems rather on trying to re-invent historic conditions; i.e., place less emphasis on reference conditions. We also need to engage in landscape and regionally scaled conservation and restoration programs in which various public actors and scientists are fully engaged. And finally, we need to invest in meaningful, long-term adaptive management of restoration projects, so that we learn as we go and are able to make timely corrections and disseminate information to other practitioners.

Although the challenges are great, successful restoration projects have taught us that ecosystems are inherently resilient if we can be sufficiently flexible as a society to give them the opportunity to flourish. The key is to couple realistic restoration expectations while creating that opportunity on a broad enough scale to sustain these species and ecosystems over time.

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CLIMATE CHANGE AND GRASSLAND RESTORATION IN CALIFORNIA: LESSONS FROM SIX YEARS OF RAINFALL MANIPULATION IN A NORTH COAST GRASSLAND

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ABSTRACT

Native perennial bunchgrasses have undergone steep declines across much of California but persist in sizable populations along the northern coast. The longer rainy season and less severe summer drought in this region are thought to facilitate bunchgrass persistence in the face of extensive invasion by exotic annual species. Changes in the seasonality and intensity of precipitation that accompany global climate change could critically influence efforts to conserve and restore these plants in California grasslands. We established a large-scale manipulation of rainfall in a protected Mendocino County grassland to investigate how predicted shifts in precipitation affect the performance of three native perennial bunchgrass species in exotic-dominated stands. We added seeds, plugs, and mature tussocks of *Danthonia californica*, *Elymus glaucus*, and *Elymus multisetus* into replicate plots of exotic annual grassland and subjected the plots to one of three experimental precipitation regimes: increased winter rainfall, increased spring rainfall, and ambient rainfall. Responses to rainfall addition varied widely by age class and species and depended heavily on seasonal timing of the increase. Establishment from seed was rare for all three species and showed little response to water addition, likely due to concomitant changes in the surrounding communities. Production of exotic annual grasses rose markedly following repeated extensions of the rainy season, and while established bunchgrasses benefited despite this change, new plants could not establish into thickening stands of exotic vegetation. In contrast, survival was high for transplanted plugs and tussocks of all three species across all three rainfall treatments, suggesting that plugs and tussocks can survive a wide range of climatic conditions and high local densities of exotic annual grasses. Restoration approaches focused on these life stages may be most robust to changing climate. Transplanted individuals can provide a continual source of propagules to surrounding areas that then recruit during years in which conditions in the physical and biological environment are amenable to seedling establishment.

Key Words: bunchgrasss, *Danthonia californica*, ecological restoration, *Elymus glaucus*, *Elymus multisetus*, perennial grass, precipitation.

Restoration of native plants in exotic-dominated grasslands is a major conservation challenge in California. Annual grass and forb species from Europe and Asia dominate most grasslands, with native perennial grass populations sparse across much of the state (Bartolome et al. 1986; Huenneke 1989; Hamilton 1997). Sizeable populations that do remain are generally restricted to northern coastal prairie sites, but even here native plants exist amid abundant exotic cover (Hektner and Foin 1977; Hayes and Holl 2003). Where native perennial bunchgrasses are abundant, they can improve summer grazing (Wagner 1989), increase ecosystem nutrient retention (Menke 1989; Adams et al. 1999), and restrict further invasion by exotic species (Peart 1989a; Corbin and D'Antonio 2004a). Conservation efforts therefore seek to establish or maintain native bunchgrass populations in the face of extensive invasion by exotic species.

Scientists and managers have evaluated techniques such as fire, grazing, and carbon addition for their ability to improve the establishment and performance of native grasses (e.g., Hatch et al. 1999; Corbin and D'Antonio 2004b; Corbin et al. 2004). Ultimately, however, the effectiveness of any management practice could be strongly influenced by climate. Extended drought in the nineteenth century is thought to have played an important role in the widespread replacement of California's native perennial grasses by exotic annual species (Major 1988; Mack 1989), and the success of native bunchgrasses along the northern coast likely stems in part from the longer winter rainy seasons and shorter summer droughts that characterize the region (Elliot and Wehausen 1974; Heady et al. 1977, 1992; Peart 1989b; Stromberg et al. 2001). Changes in precipitation

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regimes that accompany global climate change could have pronounced effects on native perennial bunchgrasses.

General circulation models developed at both the *Hadley Centre for Climate Prediction and Research* (HadCM2) and the *Canadian Centre for Climate Modeling and Analysis* (GCCM1) forecast substantial increases in precipitation throughout northern California over the next century (National Assessment Synthesis Team 2000). The two models differ, however, in the predicted seasonality of these increases. In this difference may lie considerable implications for the future of California's grasslands.

The *Hadley* model calls for the entirety of the precipitation increase to fall within California's current winter rainy season, with no effect on the length or severity of annual summer drought. Rainfall during the winter and early spring in northern California generally exceeds the amount necessary for plant growth (Pitt and Heady 1978), so winter-time increases may be largely superfluous. Effects could manifest if increased winter rainfall eliminates the mid-winter dry spells typical in northern California. Every winter rainy season in the last fifty-six years in northern California has experienced a rain-free period of at least eight and on average nineteen consecutive days (Null 2006). Established bunchgrasses have slow winter growth rates and deep root systems that buffer them from the short-term drying of surface soils that can accompany these dry spells (Holmes and Rice 1996; Reever Morgan et al. 2007), but shallowly-rooted grass seedlings can be negatively impacted (Bartolome 1979; George et al. 1985; Young and Evans 1989). Increased winter rainfall could then potentially benefit newly germinated perennial grass seedlings, but net effects would depend on the relative benefit to these plants versus their annual competitors.

The *Canadian* model projects increased rainfall extending into the spring and summer. This could have more pronounced effect on perennial bunchgrasses. California grassland communities are strongly affected by the state's Mediterranean climate, in which 95% of annual precipitation typically falls between the months of November and April (Major 1988). Late spring and summer rainfall is typically rare, but when it does occur it can increase productivity, extend the period of activity, and improve autumn regrowth of native bunchgrasses (Laude 1953; Jackson and Roy 1986). In contrast, exotic annual grasses in California maximize their productivity and reproduction at the time of high water availability in spring, senesce by mid-May, and are generally unresponsive to extensions of the rainy season beyond April (Pitt and Heady 1978; Jackson and Roy 1986). This strategy is well suited to the current climate, but would not allow exotic annuals much direct benefit from increased spring and summer rainfall associated with global change. Previous work in our study system, however, has shown that exotic annual species can benefit indirectly from extension of the rainy season via a fertilization effect caused by increased productivity and extended seasonal activity of nitrogen-fixing legumes (Suttle et al. 2007). Net effects, again, may then depend on the relative magnitude of native bunchgrass benefit versus the increased competition they could experience from stimulated annual grass productivity.

We manipulated rainfall over large plots of exotic-dominated grassland for six years to explore potential consequences of each scenario for individual- and population-level performance of three native perennial bunchgrasses.

Methods

Study System. The study was conducted at the Angelo Coast Range Reserve in Mendocino County, California (39°43′45″N, 123°38′40″W). Grasslands at this site occur on abandoned terraces of the South Fork Eel River, with soils derived from rocky mudflows across terrace surfaces. Vegetation is a well-mixed assemblage of annual and perennial grasses and forbs of both native and exotic origin. Mean annual precipitation is 216 cm (P. Steel, University of California Natural Reserve System unpublished), with the vast majority falling between the months of November and March. Local topography blocks coastal fog, so summers are hotter and drier at the study site than along the nearby coast (Johnson 1979).

Experimental Design. The experiment consisted of eighteen circular plots, each nearly 70 m^2, subjected to one of three watering treatments in a randomized design (Fig. 1). Treatments included a winter addition of water (January through March) simulating an intensification of the rainy season, a spring addition of water (April through June) simulating an extension of the rainy season, and a control in which no water was added above ambient rainfall.

Water diverted from a mountain spring and filtered to 40 microns was delivered to experimental plots using sprinklers designed to distribute water evenly over circular plots (Rain Bird® Rain Curtain™, Azusa, CA). Inorganic nitrogen concentrations in the water fall within the natural range of concentrations in ambient rainfall at the study site. The water delivery protocol was identical for the winter and spring addition treatments—valves leading to the sprinklers were actuated by battery-operated timers set to "rain" 14 to 16 mm of water on the plots approximately two hours after dawn every third day for 87 d, regardless of ambient weather. Each watered plot

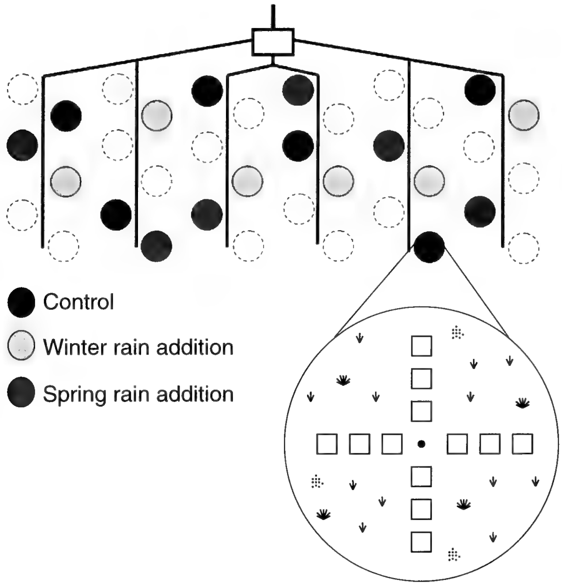

FIG. 1. Schematic of experimental design, illustrating assignment of treatments across plots and seed, plug, and tussock additions within a plot. Seeds, plugs, and tussocks were added to experimental plots at least 0.5 m away from the twelve permanent subplots used to monitor natural recruitment of native grasses. Experimental plots were approximately 70 m^2 and were separated from neighboring plots by at least 5 m. Solid lines show the layout of the buried irrigation system; circles with dotted outlines indicate plots used in separate research.

received approximately 44 cm of supplementary water per year, representing roughly a 20% increase over the long-term mean.

We examined effects of seasonal watering over six years on three native perennial C_3 grasses: *Danthonia californica*, *Elymus glaucus*, and *Elymus multisetus* (nomenclature follows Hickman 1993). All three species are widely distributed across western North America, common components of remnant and restored native grasslands, and ecologically significant in coastal prairie; *Danthonia* is considered diagnostic for the type (Heady et al. 1977). Although the three species we chose to focus on occur in close proximity within our field site, they are known to differ in their habitat associations across larger spatial scales. *Danthonia* is categorized as a facultative wetland species while the two *Elymus* taxa are not (USDA NRCS 2007). *Elymus glaucus* is often found in moderately mesic woodland and grassland sites, while *E. multisetus* is most common in drier habitats with sandy or rocky soils (Hickman et al. 1993). All three species are abundant along the edge of the study meadow but were absent from most experimental plots when the experiment was laid out. Prior to beginning the manipulation, we designated twelve permanent subplots (50 cm × 50 cm) within each plot in which to monitor natural bunchgrass recruitment across the study. We then added *Danthonia*, *E. glaucus*, and *E. multisetus* to each experimental plot as seed, "plugs" (plants of 2–3 cm basal diameter), and "tussocks" (plants of approximately 10 cm basal diameter) at least 50 cm outside of the "recruitment" subplots (Fig. 1).

Plugs and tussocks were harvested from outside experimental plots by stabbing the flat blade of an OST® Tree Planter vertically in a square pattern around each plant to 25 cm depth and prying the soil block upward. These were then transplanted into experimental plots. The size and planting method used for plugs make them approximations of the individuals grown for use in restoration projects, but ours were likely older. Transplanting large tussocks may not be a viable restoration approach at large spatial scales, but could be used in small areas to overcome local propagule limitation (Sheley and Krueger-Mangold 2003), a potential problem in some California grassland sites (Hamilton et al. 1999; Seabloom et al. 2003a).

We transplanted four plugs of each species into experimental plots in December 2000, capitalizing on conditions of high soil moisture. We monitored survival of these plants annually until March 2005, at which time we measured the basal diameter of tussock vegetation for comparison of plant sizes across watering treatments. Tussock vegetation was bunched tightly in hand immediately above the ground surface, and digital calipers were fitted around the tight vegetative bunch.

In August 2001, we sowed seeds of each species into separate 25-cm × 25-cm areas of intact vegetation or disturbed bare soil within each experimental plot. For each seed addition, we added 50 seeds collected from seed heads of plants at the study site. For *D. californica*, we also added five basal culm sections, because this species produces cleistogamous florets in its flowering culm bases in addition to distal seeds. DiVittorio et al. (2007) measured mean native perennial grass seed rain of 620 seeds m^{-2} (range = 0–2200) across a gradient of native perennial grass cover in another northern California coastal prairie site, so our seed densities (800 seeds m^{-2}) are consistent with natural inputs. Subplots were surveyed for seedling establishment during the following summer. We repeated seed additions in new areas within each plot in August 2003 and surveyed these in summer 2004.

In December 2001, we transplanted mature *E. glaucus* and *D. californica* tussocks into experimental plots. *Elymus multisetus* was initially excluded owing to concerns over its scarcity in the meadow, but following large recruitment in 2001 and 2002, we transplanted a mature tussock of this species in December 2002. We measured tussock reproductive output by counting the

TABLE 1. TOTAL NUMBER OF SEEDLINGS OF THREE NATIVE GRASS SPECIES THAT ESTABLISHED IN RESPONSE TO SEED ADDITION ONTO 25-cm BY 25-cm STANDS OF INTACT VEGETATION AND DISTURBED SOIL ACROSS ALL WATERING TREATMENT PLOTS IN 2002 AND 2004.

		Control		Winter +		Spring +	
	Species	Vegetation	Soil	Vegetation	Soil	Vegetation	Soil
2002	*Danthonia*	0	0	0	0	1	1
	E. glaucus	0	0	0	0	3	2
	E. multisetus	1	na	3	na	3	na
2004	*Danthonia*	1	1	2	2	0	4
	E. glaucus	0	0	0	1	0	4
	E. multisetus	2	na	3	na	1	na

flowering culms produced each summer. We measured leaf carbon dioxide and water vapor exchange rates of planted tussocks using a LI-6400 portable photosynthesis system (LI-COR, Lincoln, NE) in early June 2003. *Danthonia californica* and *E. glaucus* tussocks were sampled in all plots, but *E. multisetus* had senesced by this date in one ambient and one spring-watered plot, so only 16 individuals were measured. Measurements were taken within two hours of solar noon on two consecutive sunny days. Chamber conditions were set to 400 ppm CO_2, 1000 $\mu mol/m^2/s$ photosynthetically active radiation, 25°C, and ambient humidity. Sampled leaf portions were collected and their areas determined using a LI-3100C leaf area meter (LI-COR, Lincoln, NE). Leaf area values were used to correct gas exchange values and calculate per leaf area photosynthetic rate and water use efficiency (WUE) for each individual.

Finally, we counted native bunchgrasses in all permanent subplots inside each plot in January 2007 to assess how the different rainfall regimes had impacted the recruitment of new plants into stands of exotic-dominated vegetation over the previous six years.

Statistical Analyses. The rarity of establishment from seed for any of the three species precluded statistical testing for effects of watering treatment within a single species or for differences in establishment between intact vegetation and disturbed soil. We tested for watering treatment effects on survival, growth, reproductive output, photosynthetic rate and WUE of each species separately, using one-way ANOVA, followed by Tukey tests when significant treatment effects were detected. We conducted the ANOVA of plug size in 2005 on plot-wide means for all surviving plants of each species, having eliminated from the analysis plots with no surviving plugs for a given species. Proportional plug survival data were arcsine-square root transformed and tussock culm production data were square root transformed prior to analysis to meet assumptions of normality and equality of variances. We tested for time by treatment interactions in flowering culm production across years with repeated measures ANOVA. After this analysis revealed no significant time by treatment interactions ($P >> 0.10$), we condensed reproductive data by calculating average culm production for each plant across all years of measurement.

RESULTS

Seed and plug additions. Seedling establishment was rare following either year of seed addition: a total of fourteen and twenty-one seedlings established in 2002 and 2004, respectively (see Table 1 for treatment and species totals). Across both years, five seedlings established in ambient rainfall plots, eleven in winter water addition plots, and nineteen in spring-watered plots.

Spring water addition more than doubled the survival of the four *D. californica* plugs planted per plot relative to winter-addition and ambient conditions ($F_{2,15}$ = 11.03, $P < 0.01$) (Fig. 2). There was a nearly-significant increase in *E. glaucus* survival in spring-watered plots ($F_{2,15}$ = 3.64, $P = 0.052$), but no effect of watering treatment on *E. multisetus* ($F_{2,15}$ = 0.57, $P > 0.10$).

Treatment effects on vegetative growth of plugs were likewise apparent for only two of the three species. *Danthonia californica* plants grew approximately twice as large in spring-addition plots as in winter-addition or control plots ($F_{2,15}$ = 13.81, $P < 0.001$), while *E. glaucus* plugs were more than three times larger in winter and spring water addition plots than in ambient control plots ($F_{2,15}$ = 9.72, $P < 0.01$; Fig. 2). *Elymus multisetus* growth did not respond to watering treatment ($F_{2,15}$ = 1.71, $P > 0.1$).

Reproductive output and physiology of mature tussocks. All mature tussocks transplanted into plots survived through the duration of the experiment. Spring water addition increased production of flowering culms in both *D. californica* ($F_{2,15}$ = 6.34, $P = 0.01$) and *E. glaucus* ($F_{2,15}$ = 11.24, $P < 0.01$) relative to winter addition and control conditions (Fig. 2). Both species pro-

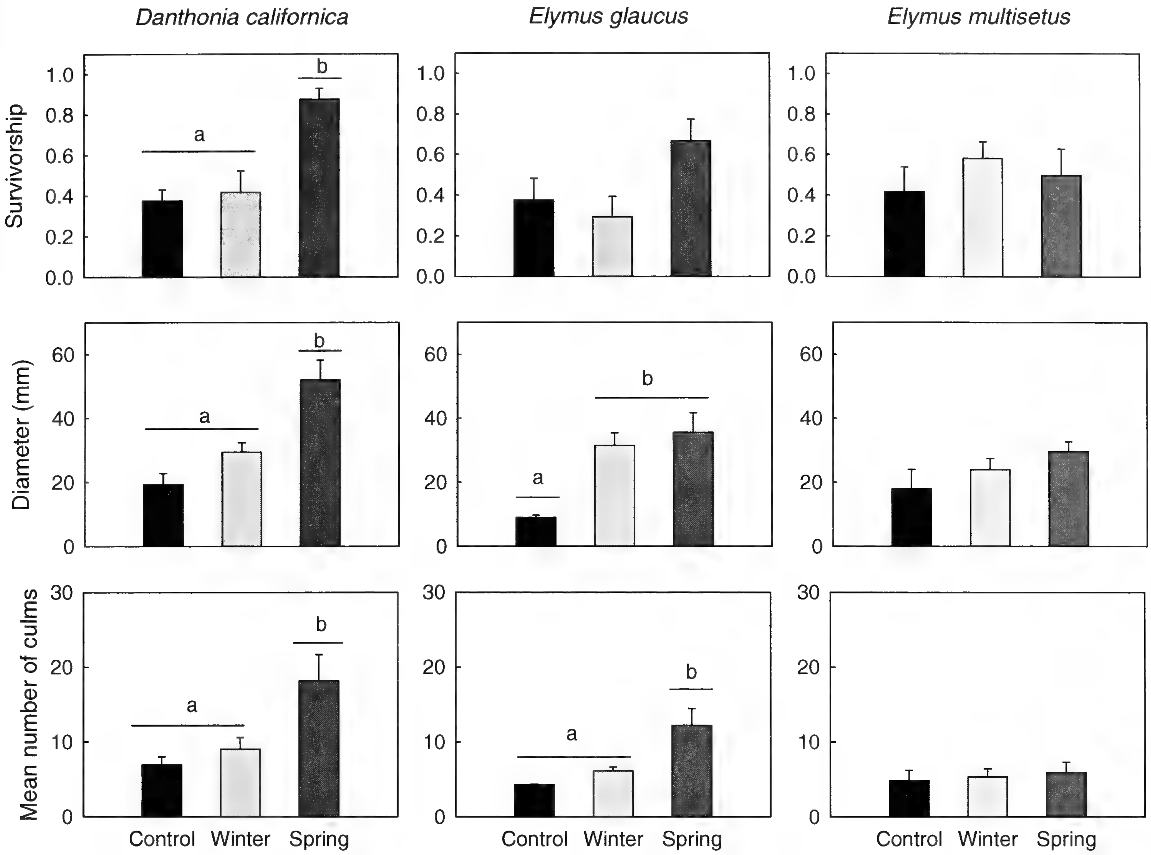

FIG. 2. Watering treatment effects on the proportional survivorship and growth of plugs and the mean reproductive output of mature tussocks of three native grass species across five years of rainfall manipulation. Letters indicate statistically significant differences between treatment groups revealed in *post hoc* Tukey tests.

duced about twice as many culms when receiving additional spring rainfall than under winter-addition or ambient rainfall conditions. There was again no response from *E. multisetus* ($F_{2,15}$ = 0.24, P > 0.1).

Watering treatment had a significant effect on photosynthetic rates of all three species (*D. californica* $F_{2,15}$ = 7.63, P < 0.01; *E. glaucus* $F_{2,15}$ = 3.69, P < 0.05; *E. multisetus* ($F_{2,13}$ = 5.22, P < 0.05; Fig. 3). Spring water addition increased *D. californica* carbon gain per unit leaf area by more than 70% relative to ambient or winter water addition conditions. In contrast, *E. multisetus* individuals in winter addition plots had approximately 40% lower photosynthetic rates than those in ambient or spring water addition plots. Photosynthesis of *E. glaucus* individuals across watering treatments did not differ significantly in *post hoc* tests.

Water use efficiency varied significantly with watering treatment for both *Elymus* species (*E. glaucus* $F_{2,15}$ = 8.36, P < 0.01; *E. multisetus* $F_{2,13}$ = 5.20, P < 0.05; Fig. 4) but not for *D. californica* ($F_{2,15}$ = 1.95, P > 0.10). The average WUE of *E. glaucus* plants in ambient and winter water addition plots was greater than that of individuals in spring-watered plots (7.1 vs. 3.9 mmol C mol H_2O^{-1}). For *E. multisetus* individuals, the WUE of individuals experiencing ambient conditions was intermediate (5.3 mmol C mol H_2O^{-1}) between those in winter- and spring-watered plots (7.4 and 4.6 mmol C mol H_2O^{-1}, respectively).

Population-level recruitment. Over six years, natural recruitment of new plants into exotic-dominated stands was low across species and absent altogether for *Elymus glaucus*. *Danthonia californica* and *Elymus multisetus* did revegetate portions of the grassland, but not in a manner that varied with watering treatment. Across the twenty-four experimental plots in which native grasses accounted for <5% of ground cover at experiment's start (including plots not included in the research described here—see Fig. 1), mean recruitment was actually highest in control plots (Fig. 4), although highly variable and with no significant difference among treatments. An average of 3.5 ± 1.7 (mean ± 1 SE) new bunchgrass recruited into the 3 m^2 of vegetation (12 subplots × 0.25 m^2 each) monitored in each

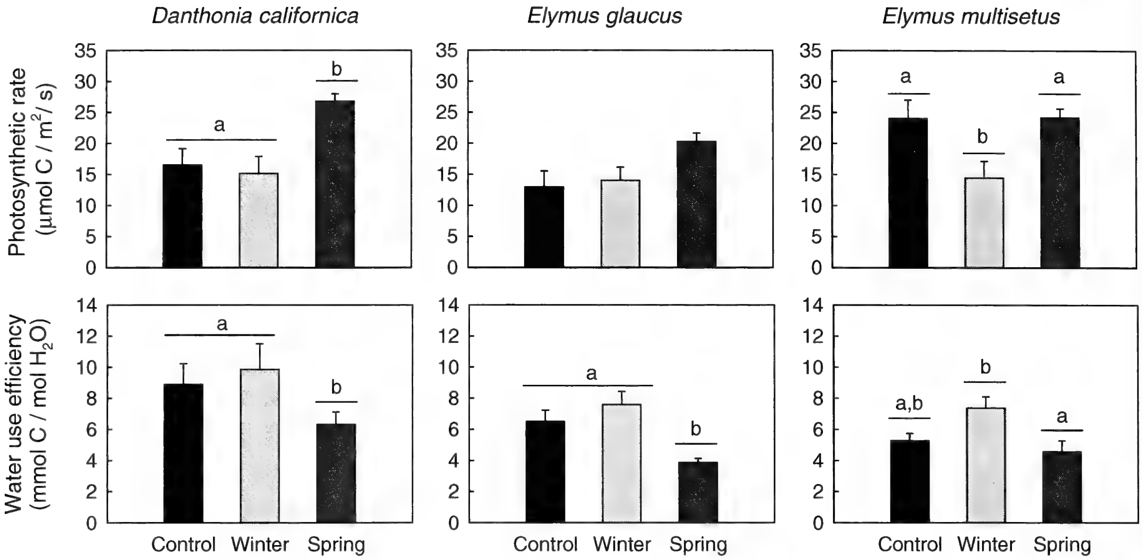

FIG. 3. Effect of watering treatment on tussock photosynthetic rate and water use efficiency in June 2003, two months after the end of winter water addition and the beginning of the spring watering treatment. Letters indicate statistically significant differences between treatment groups revealed in *post hoc* Tukey tests.

control plot, with 1.1 ± 0.6 new plants in winter-addition and 2.9 ± 1.0 new plants in spring-addition plots.

Exotic annual grasses. Effects of water addition on other plant species and on higher trophic levels are described in detail elsewhere (Suttle et al. 2007). It is noteworthy here to state that the favorable responses to spring water addition by established *Danthonia* and *Elymus glaucus* plants occurred alongside marked increases in the production of exotic annual grass species such as *Bromus hordeaceus* and *B. diandrus*. These annual grasses showed little direct response to water addition, occurring at similar biomass across all three treatments through the first year of the experiment. In subsequent growing seasons, however, they appeared to benefit strongly from a fertilization effect driven by the nitrogen-fixing *Lotus micranthus*. Following dramatically increased production and extended longevity of this legume in spring-watered plots in one year, annual grass production and tissue nitrogen concentrations rose markedly in the next. As this cycle was repeated again and again, annual grass biomass in spring-addition plots came to more than double that in control and winter-addition plots in some years (Suttle et al. 2007).

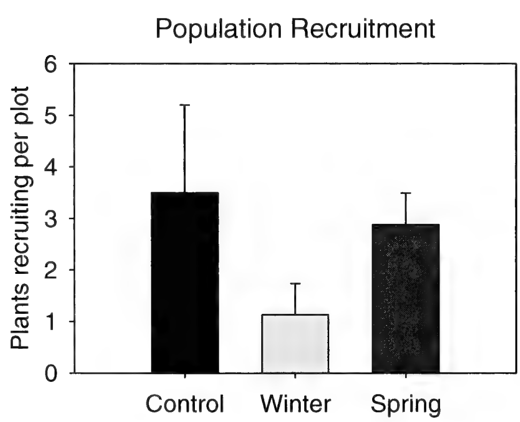

FIG. 4. Effect of watering treatment on population-level recruitment by native grasses into experimental plots over six years of rainfall manipulation. Data represent mean + SE) number of new individual bunchgrasses recruiting into the permanent subplots arrayed through each experimental plot between 2001 and 2007.

DISCUSSION

Information on how climate change will impact species and habitats is urgently needed, both to improve our understanding of specific threats and to guide allocation of limited conservation resources in addressing them. In California, changes in precipitation regimes that accompany global climate change could have profound consequences for grassland structure and species composition, but with impacts varying by species and life stage, tied strongly to seasonal timing, and propagating widely through interaction webs, reliable predictions of these consequences will be difficult to attain. Predictions based on generalized life history differences between native and exotic plants are clearly insufficient. This prudence gains further support as perceptions change over the original native composition of these systems, with re-

searchers coming to appreciate that annual forbs were important original components of California's grassland landscapes (Jepson 1925; Hamilton 1997—see Seabloom et al. 2003b for a study of native forb restoration). The native perennial/exotic annual dichotomy is made more obsolete as exotic perennial bunchgrasses such as *Holcus lanatus* and *Anthoxanthum odoratum* become increasingly abundant along California's northern coast. Through other work in this study system, we have found that increased spring water availability strongly favors establishment and survival of *Holcus lanatus* and could facilitate its spread into new areas (Thomsen et al. 2006).

Many authors have already commented that geographic origin alone is not a biologically significant characteristic, making it unwise to expect native versus exotic species to exhibit consistent responses to the environment and to other species (e.g., Levine and D'Antonio 1999; Davis et al. 2001). Similarly, several California researchers have argued against the tendency to treat *Nassella pulchra*, a prominent focus of California grassland research and restoration efforts, as broadly representative of the state's native bunchgrasses (Huntsinger et al. 1996; Hamilton 1997; Hatch et al. 1999). Our results support this call for caution when generalizing across California's perennial bunchgrass species, demonstrating that these may respond in disparate ways to changing precipitation regimes.

As predicted by life history characteristics, spring watering increased the survivorship, growth, and reproductive output of *D. californica* and *E. glaucus*. In contrast, winter water addition had little effect on any measure of their performance, including seedling establishment, which we predicted might be positively influenced by amelioration of mid-winter dry spells. *Elymus multisetus*, meanwhile, showed no response to either watering treatment in any measured response. Adaptations that allow *E. multisetus* to survive in extremely dry conditions may be present at the expense of those that would allow favorable responses to unusually high moisture levels.

Our measurements of summertime plant physiology provide some insight into these differing responses. *Danthonia* and *E. glaucus* had higher photosynthetic rates and lower water use efficiencies in spring-addition plots than under ambient and winter-addition treatments. Thus spring water addition, as expected, extends the active growing season for these species. In contrast, *E. multisetus* tussocks had comparably high photosynthetic rates in control and spring-addition plots, and significantly lower carbon gain in winter-addition plots. Water use efficiency followed a complementary pattern, with greater efficiency in winter-addition plots than in control or spring-addition plots. Further research is needed to determine the specific mechanisms underlying these differing responses to water availability.

In general, however, once established in experimental plots all three species fared well regardless of treatment conditions. For transplanted plugs, at least some individuals of every species survived in nearly every plot. These survival rates are high relative to studies that followed young native grass recruits from seed in exotic-dominated grasslands (Dyer et al. 1996; Dyer and Rice 1997; Hamilton et al. 1999; Brown and Rice 2000), presumably because the 2–3 cm diameter plants we harvested for transplant were older. Corbin and D'Antonio (2004a) found that three-month-old native grass seedlings survived well when transplanted into dense plots of exotic annual grasses, supporting the finding here that plugs may be a more effective restoration technique for native grasses than seed additions. Furthermore, the 100% survival of large tussocks that we transplanted into experimental plots agrees with previous work showing that mature natives compete well in exotic-dominated California grasslands (Peart 1989a; Corbin and D'Antonio 2004a).

The strong performance of established individuals may not translate clearly to improved population-level performance, however. Establishment following seed addition was rare across all treatment conditions, in line with previous research showing native California bunchgrasses to be most vulnerable at the seedling stage to competition from surrounding plants (Peart 1989b; Dyer et al. 1996; Dyer and Rice 1997; Hamilton et al. 1999; Brown and Rice 2000; Corbin and D'Antonio 2004a,b), and recruitment from seed to be low even where sizeable bunchgrass populations exist (Bartolome and Gemill 1981; Peart 1989b). We measured seedling establishment after only two years of seed addition, but across the full six-year experiment both *Danthonia* and *Elymus multisetus* seedlings have begun to appear in plots from which they were absent at experiment's start (K. B. Suttle personal observation).

Seedling recruitment will be heavily influenced by the specific climate and surrounding plant assemblage each year, and the interactive effects of these factors warrant further study. Established bunchgrasses, on the other hand, can persist through a wide range of climatic conditions and competitive environments, seeding the surrounding area with propagules over many years or decades. Revegetation of exotic-dominated stands via recruitment from these propagules may proceed slowly, but given the high interannual variability in climate and grassland standing crop and species composition characteristic of California, sporadic bursts of revegetation can be expected. Restoration approaches that focus on individual transplants should thus be fairly robust

to environmental change. Given the complexities of climatic and ecological prediction, maximizing robustness of restoration measures to a wide range of conditions should be a foremost goal.

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EMERGING ISSUES FOR THE RESTORATION OF TIDAL MARSH ECOSYSTEMS IN THE CONTEXT OF PREDICTED CLIMATE CHANGE

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ABSTRACT

There is currently a large regional effort to restore tidal marsh ecosystems in the San Francisco Bay-Delta Estuary involving the commitment of hundreds of millions of dollars and broad landscape-scale habitat manipulations. Although climate change has been on the horizon for many years, recent developments suggest that it must be taken seriously as a factor to be considered in future planning for marsh restoration efforts. Tidal marshes are vulnerable to changes in salinity and inundation rates, both of which will be affected by climate change. Restoration sites may be particularly vulnerable given unpredictable sediment inputs and newly established vegetation. Predicted shifts in snowmelt and altered runoff will change estuarine salinity patterns and could have large-scale impacts on marsh dominance, especially for freshwater marshes. Even relatively small salinity changes could lead to shifts in dominant species, with freshwater marshes being replaced by brackish marshes and brackish marshes converted to salt marsh communities. This will cause a reduction in overall estuarine plant diversity and productivity, with possible reverberations for the estuarine food web. Based on monitoring data from San Francisco Bay marshes, we predict that salinity will have a more immediate impact on tidal marsh vegetation than sea-level rise. However, sea-level rise poses a potentially greater long-term threat, depending on its rate, because the effects of inundation and a more persistent salinity regime could cause widespread marsh loss. If ice sheets in Antarctica and Greenland begin melting at rapid rates, inundation impacts could be catastrophic for coastal marshes. Given the magnitude of these potential changes, we urge the restoration and conservation management community to integrate these contingencies into adaptive management process and to join with the broader community in forging more flexible governance institutions that can respond effectively to large-scale uncertainties and trajectories as they unfold.

Key Words: brackish marsh, climate change, freshwater tidal marsh, inundation, salinity, salt marsh, *Sarcocornia pacifica*, sea-level rise, *Spartina foliosa*.

Growing evidence suggests climate change will have an impact on virtually all ecosystems (Walther et al. 2002). While climate change models have generated a wide range of predictions, a consensus indicates a few critical shifts could affect specific ecosystems, particularly tidal marshes. First, the rise in average global temperatures will influence the timing and degree of snowfall and ice melt, shifting temporal runoff patterns in watersheds dominated by mountain snowpack. Second, rates of sea-level rise are almost certain to increase over the next several decades. Sea-level rise will push sea water farther up into estuaries, increasing salinities in tidal ecosystems. Tidal marshes are likely to be particularly vulnerable to climate change impacts through these shifts in salinity and inundation patterns. For a region like the San Francisco Bay-Delta estuary (hereafter, SF Estuary), less snow and earlier melting of the Sierra snowpack will result in higher floodwaters during winter and early spring but lower flows during late spring and summer. These changes will amplify seasonal and spatial shifts in estuarine salinity patterns, impacting wetland plant establishment, productivity, and reproduction. In addition, tidal marshes will have to accumulate substantial sediment to counteract sea-level rise, or they will be subjected to greater stress associated with longer periods of tidal inundation. The overall influence of climate change, therefore, is a combination of changes in inundation and salinity regimes, with impacts on plant communities and the ecological function of tidal marshes.

Against this backdrop of global climate change and its regional manifestations, large-scale efforts are underway to restore tidal marsh ecosystems, and these initiatives are particularly strong in the SF Estuary. In this paper, we examine tidal marsh restoration in the SF Estuary in the context of climate change and explore the

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potential impacts and vulnerabilities of marsh restoration projects in view of these predicted changes. Our aim is to draw attention to these contextual factors so that they can be more effectively evaluated and mitigated as tidal marsh restoration planning and implementation efforts go forward.

Tidal Marsh restoration

The science of restoration ecology and the practice of ecosystem restoration have grown dramatically over the last decades for a variety of reasons (Falk et al. 2006). Tidal marshes have received considerable restoration attention because many coastal ecosystems have been severely impacted by human modifications and development, with loss of both habitat acreage and function. Within California, for example, over 90% of coastal salt marsh and tidal freshwater marshes have been affected by agriculture, the salt pond industry, airports, and urban development. The recent focus on restoration is evidenced by the number of recent, large-scale projects within the SF Estuary, including the South Bay Salt Pond Restoration Project (over 6000 ha of salt ponds slated for restoration and management), North Bay salt pond restoration, Montezuma wetlands, Sonoma Baylands, Hamilton wetlands, and others. In addition to these large-scale projects, many smaller mitigation projects have occurred throughout the Bay over the last two decades (see www.wetlandtracker.com for mapping of many projects). Most restoration work has focused on salt marsh restoration, with additional large-scale efforts recently undertaken for the SF Estuary's brackish and freshwater tidal marshes through CALFED-funded projects. Similar large- and small-scale efforts exist in southern California, Oregon and Washington.

A major biological focus of marsh restoration efforts has been to maximize plant establishment. In California salt marshes, two dominant species are emphasized, *Spartina foliosa* Trin. (California cordgrass), found along channels and in a narrow band at the low end of the marsh, and *Sarcocornia pacifica* (Standl.) A. J. Scott (pickleweed; formerly *Salicornia virginica* L.), dominant on the marsh plain. In general, the design of restoration projects focuses on elevation as the key factor influencing plant distributions, due to its relation to tidal dynamics and consequently to within-marsh patterns of inundation, anaerobiosis, and salinity. These physical processes appear to be the most important in tidal systems, sorting species by their tolerance to various combinations of these stresses (Mahall and Park 1976a, b, c), although zonation into low and high marsh is an oversimplification of real patterns of vegetation distributions within the marsh (Zedler et al. 1999). Competition and other biological interactions are also important in affecting overall distributions (Pennings and Callaway 1992; Grewell et al. 2007).

Given the focus on elevation as the overall driving force for plant distributions, the approach in early restoration projects was simplistic. Sites were graded to target elevations, and most early restored marshes were designed with a gradually sloping profile from the low marsh through the mid-high marsh. Target elevations across the marsh were based on surveys of plant distributions from nearby natural marshes or from general regional information on elevational distributions. In some cases, propagules (plants, seeds, or cuttings) were introduced to establish appropriate vegetation, in particular for *S. foliosa*; however, in many cases plants were expected to recruit naturally. Restoration projects also were designed without the network of small tidal creeks that are critical to natural marsh dynamics (Zedler et al. 2001; Wallace et al. 2005; Zedler 2005), despite the fact that creeks clearly affect plant distributions (Zedler et al. 1999; Sanderson et al. 2000). Upland transition zones in these restoration projects were often steep and narrow in order to maximize marsh area, a practice that highlights the strong influence of policies that do not count transitional areas or uplands as credit towards mitigation acreage. Maintaining or increasing habitat of rare listed species, such as the Light-footed and California Clapper Rails, has always been one of the key considerations for marsh restoration projects; however, creating this habitat has been difficult (Zedler 1998). Simplistic approaches towards restoration ran into a number of challenges, including, but not limited to incorrect substrate condition (often too coarse, with little organic matter and low nutrient concentrations, especially when using dredged material to build elevations); slow recruitment of native vegetation; invasive plants (in particular *Spartina alterniflora* Loisel. and its hybrids with *S. foliosa* in SF Estuary); unpredictable hydrological complications; improper elevations; and erosion from wind-driven waves across flooded sites (Zedler and Callaway 2000; Williams and Faber 2001; Callaway 2005).

As a response to some of these challenges, there have been shifts in recent restoration designs for tidal marshes. For example many restoration sites are now established at elevations slightly below target elevations for plant recruitment to allow for natural sediment accumulation throughout the rooting zone of marsh vegetation and to stimulate development of tidal creeks (Williams and Orr 2002). This approach has been particularly popular in the SF Estuary where high concentrations of suspended sediment ensure relatively rapid and consistent rates of

sediment accumulation. In Tijuana Estuary, substantial efforts have been made to incorporate experimentation into restoration projects in order to improve restoration design and improve understanding of controls on marsh functioning (Zedler 2001). The Tidal Linkage project focused on the link between plant species diversity and ecosystem functions in restored salt marshes (Zedler et al. 2001; Callaway et al. 2003; Sullivan et al. In Press), while Friendship Marsh, an 8-ha project in the south arm of Tijuana Estuary, has evaluated the importance of tidal creek networks (Wallace et al. 2005). As our understanding of wetlands increased and the significance of linkages to terrestrial and aquatic ecosystems became clearer, the goal of tidal marsh restoration has evolved from the more narrowly focused goals of plant establishment and endangered species towards the maintenance and expansion of community structure, food web dynamics, and ecosystem function. This trend is especially evident in large-scale projects that are not constrained by mitigation issues.

Recently restored tidal marshes are likely to be particularly vulnerable to impacts related to climate change. While shifts in vegetation communities in older marshes will be buffered by the existence of well-established vegetation, recently restored sites lack dense vegetation cover, and new sites have no vegetation at all. Recruitment patterns will determine dominant vegetation in newly restored sites, and recruiting plants are likely to be more vulnerable to extreme events. Therefore, climate-induced shifts in salinity and/or inundation regimes are more likely to cause rapid vegetation shifts at newly restored sites. Reinforcing potential shifts in vegetation establishment, the lack of vegetation at newly restored sites increases surface evaporation and can increase surface soil salinity to the point of salt crust formation in poorly flushed areas of restored sites, leading to even higher salinity stresses (Zedler et al. 2003).

Compared to natural marshes, restored marshes are at a disadvantage under a tidal regime of higher sea level and longer inundation periods. Not only will restored marshes have to keep pace with increased rates of sea-level rise, they also will have to accumulate additional sediment in order to build elevation. Newly restored sites must increase elevation to a point where vegetation is able to colonize the restoration site. Older restored sites may have vegetation established but often need to increase elevation to get to typical marsh plain elevations of mean higher high water (MHHW). Excessive inundation will be especially problematic at highly subsided sites, which are quite common in SF Estuary. Sites that are designed at lower initial elevations with the expectation that they will build up sediment over time also could be particularly vulnerable.

Climate Change Impacts

As alluded to above, the impacts of climate change on tidal marsh restoration in the SF Estuary will involve primarily changes in salinity and inundation regimes. In the following section, we develop more detailed insight into the basis for this concern.

Causes of Salinity Changes

As climate change progresses, estuarine salinities (and soil salinities in adjacent tidal marshes) will be affected by shifts in three primary factors: (1) total regional precipitation, (2) seasonal timing of precipitation and runoff patterns (in particular shifts in the amount of snow vs. rainfall and shifts in snowmelt periods), and (3) increases in sea level. Increases in evapotranspiration also have the potential to increase soil salinity, although this is difficult to quantify. There has been substantial debate on what type of changes may occur in terms of total regional precipitation within the state. Dettinger (2005) reviewed a number of the various models and scenarios. While the perception has been that precipitation could change much more than temperature based on model projections, Dettinger (2005) found that projected temperatures spread more widely than projected precipitation in relative terms.

Despite the lack of agreement over what might occur in terms of total precipitation, there is a general consensus that warmer temperatures associated with climate change will lead to less snowfall, more rain, and earlier snowmelt throughout California (Gleick 1987; Gleick and Chalecki 1999; Knowles and Cayan 2002, 2004; Dettinger et al. 2004; Dettinger 2005). In combination, these factors will lead to much earlier runoff within California watersheds, regardless of any changes in total precipitation within the state or region. Stewart et al. (2005) have documented shifts of 1–4 wks in annual spring flows in areas of the western United States. In addition, Stewart et al. (2004) predict substantial shifts in the timing of snowmelt, with a shift of 30–40+ days toward earlier snowmelt in much of the western United States by 2100. This shift will be due primarily to increases in springtime temperatures rather than any predicted shift in regional precipitation patterns. Dettinger (2005) found that predictions of extremely wet conditions in California are extreme outliers based on current projections for climate change. Future scenarios that result in the warmest predictions indicate slightly drier conditions, while those that predict the least warming indicated slightly wetter conditions.

Malamud-Roam and Ingram (2004) and Malamud-Roam et al. (2006) examined stable isotope

data and pollen records from the SF Estuary marsh sediments during the late Holocene and correlated their findings to broader temperature and precipitation patterns in western North America. They found three major periods of higher-than-average salinity in marshes of the SF Estuary that correlated to reductions in fresh water flows during prolonged droughts. Periods of higher-than-average salinity occurred between 1600–1300 cal yr B.P., 1000–800 cal yr B.P., 300–200 cal yr B.P., and from A.D. 1950 to present (Malamud-Roam and Ingram 2004). According to Byrne et al. (2001), the recent increase in Bay salinities is likely caused by damming and diversions of water. Critically, the climate change predictions of shifts in freshwater inflows to the bay and associated salinity changes do not reflect any future increases in human water use, despite the fact that there is near certainty that there will be large increases in California population and water demands. Future increases in human water use are highly likely to reduce any increases in winter/spring inflows and further exacerbate summer reductions in flow.

In addition to salinity shifts due to changes in precipitation and runoff, there will be increases in estuarine salinities due to higher sea level. As sea level rises, it will push more saline water farther into estuarine systems. Uncles (2003) used a hydrological model to evaluate the potential effect of sea-level rise alone (without any change in freshwater inputs) on salinities within SF Estuary. The model predicts salinity shifts based on the location of the 2 ppt bottom isohaline within SF Estuary, known as "X2." X2 is an indicator of the location of the interface between incoming fresh water from the Sacramento and San Joaquin Rivers and salt water from the ocean; it shifts seasonally and annually depending on inflow conditions. Uncles (2003) found that a 25-cm increase in sea level would result in a mean shift of X2 by 1 km upstream, with a maximum shift in some years of 3.5 km. A 50-cm increase in sea level resulted in a mean shift of 1.5 km with a maximum shift of 5.0 km, and a 100-cm increase caused a mean shift of 3 km and a maximum shift of 9 km. These model results indicate that substantial shifts in salinity could occur year round due to sea-level rise, and these changes would be additive to any effects due to shifts in watershed runoff.

Salinity Effects on Vegetation

The changes in salinity due to precipitation, runoff, and sea-level rise will have variable effects on vegetation. The lower salinities that are predicted in the winter and early spring will affect plant recruitment in restored marshes. Larger pulses of winter fresh water could increase recruitment for many species, as most salt and brackish marsh vegetation responds positively to freshwater pulses and reductions in salinity (Ungar 1978, 1991; Noe and Zedler 2001a). Allison (1992) found that increases in late spring rainfall led to increased diversity in salt marshes adjacent to Bolinas Lagoon. Although lower winter and early spring salinities may increase recruitment within salt and brackish marshes, it is not clear how these newly recruited plants might fare with increased salinities in summer and fall. They may not be able to reproduce or survive higher salinities during the growing season, and the influence of more extreme inter-annual variability that is likely with climate change is also very difficult to evaluate.

Higher salinities in the summer and fall will lead to greater stresses on vegetation, leading to reduced productivity and potential mortality (Callaway and Sabraw 1994; Noe and Zedler 2001a, b). In addition, soil salinities within tidal marshes are higher than water salinities within an estuary due to salt accumulation through evapotranspiration; while tidal flushing removes some of the salt, salt accumulates in the soil. This increase in soil salinity will be greater at higher elevations across the marsh, as higher areas are flushed less regularly by the tides and are exposed to surface evaporation for longer periods. As overall salinity within the Bay increases and more salts accumulate in tidal marsh soils, larger pulses of freshwater of greater duration will be required to reduce soil salinities in the marsh and promote germination and recruitment.

Data from a severe drought in 1976–77 indicate that salinity shifts can lead to large-scale changes in plant communities within SF Estuary. Atwater et al. (1979) documented a decrease in both the abundance and height of bulrush species (*Schoenoplectus americanus* (Pers) Volkart ex Schinz & R. Keller, *Schoenoplectus californicus* (C. A. Mey.) Soják, *Schoenoplectus acutus* (Mohl. ex Bigelow) Á. Löve & D. Löve, and *Bolboschoenus maritimus* (L.) Palla [names reflect recent changes in nomenclature in the genus *Scirpus*]) near Carquinez Strait during the drought with the subsequent invasion of these areas by *S. pacifica*. Salinities within the Bay near the eastern end of Carquinez Straits increased from below 10 ppt to 15–20 ppt during this period. Collins and Foin (1992) noted the spread of *S. foliosa* upstream in the north Bay during drought periods, and Malamud-Roam et al. (2006) found similar patterns of vegetation shifts in their synthesis of data from cores over a scale of hundreds to thousands of years. In other regions, similar effects from salinity shifts associated with droughts have been found. In southern California, a severe drought led to increased mortality of *S. foliosa* and long-lasting shifts in the community composition (Zedler et al. 1986). A drought in 2000 led to shifts of up to 5–10 km in

dominant tidal marsh plant communities in Louisiana. Salinities were elevated 3–10 ppt throughout the growing period in Barataria Basin (625,000 ha study area) with large-scale changes in marsh distribution from 1997 to 2000. This included an increase of 8900 ha of salt marsh and 15,900 ha of brackish marsh, and loss of 15,600 ha of fresh marsh and 9200 ha of intermediate marsh (Visser et al. 2002). Shifts were greatest in the marshes that were near large bodies of open water. Measurements from a low salinity area near Lake Pontchartrain, Louisiana during this same drought showed that mean annual salinities ranged from 0–3 ppt over a 50 yr period but were 6.5 ppt in 2000, and higher salinities could affect plant productivity and marsh stability at these sites (Thomson et al. 2001). Greenhouse evaluations of salt pulses with Gulf Coast species have shown that one to three month exposure of elevated salinities ranging from approximately 6 to 12 ppt can lead to shifts in species dominance of oligohaline (0.5 to 5 ppt) marsh species (*Sagittaria lancifolia* L., *Eleocharis palustris* (L.) Roemer & J. A. Schultes, *S. americanus*, and *Panicum hemitomon* J. A. Schultes) (Howard and Mendelssohn 1999, 2000).

Given these historic data and short-term greenhouse effects, droughts or other extreme events associated with climate change could have large-scale effects on marsh vegetation. Droughts are not a direct analog to predicted changes in San Francisco Bay salinities since predictions call for lower late spring/summer runoff but higher winter/early spring runoff; however, increased inter-annual variability in precipitation is likely with climate change (e.g., enhanced El Niño-Southern Oscillation [ENSO] events). The effects of salinity increases associated with pulses of salt water intrusion are likely to be greatest on freshwater vegetation sensitive to small shifts at the low end of the salinity spectrum. This would indicate that any salinity impacts from climate change are likely to be observable first in freshwater marshes in the western delta that are bordered by brackish conditions.

Implications of Salinity Changes for Marsh Restoration

With respect to restored marshes, impacts from salinity shifts or pulses will be greater on newly recruiting plants than on well-established vegetation. Deegan et al. (2005) evaluated shifts in both salinity and inundation regimes on both mature plants and seedlings for two brackish marsh species in Ireland. Mature plants survived but had reduced growth and reproduced at high salinities (10 ppt), while all seedlings died after one week at this salinity level (Deegan et al. 2005). Higher salinities also reduced emergence of most oligohaline species that were tested from Louisiana seed banks (including *S. lancifolia*, *Polygonum punctatum* Elliot, *Eleocharis parvula* (Roemer & J. A. Schultes) Link ex Bluff, Nees & Schauer, and *Cyperus odoratus* L.) with few species establishing at salinities above 4 ppt (Baldwin et al. 1996). While general predictions indicate the likelihood of greater freshwater inflows to estuaries and reductions in water salinity in winter and spring during recruitment periods, there is also the potential for shifts in extreme conditions associated with climate change. This could cause increased droughts or extremely wet years with very unpredictable effects on long-term trends in vegetation and recruitment.

Within a marsh, salinity impacts are likely to be greatest in the upper marsh due to greater accumulation of salts through evapotranspiration and infrequent flushing, especially during summer months. An indication of the increased effect of salinity in the upper marsh can be seen in the composition of the high marsh in both salt and brackish marshes in SF Estuary. Whereas the low marsh species are typically different (*S. foliosa* in salt marshes and *Schoenoplectus* spp. in brackish and freshwater marshes), there are many similarities in high marsh species (e.g., *S. pacifica*, *Distichlis spicata* (L.) Greene, *Atriplex triangularis* Willd., *Jaumea carnosa* (Less.) A. Gray, *Triglochin maritima* L., *Grindelia stricta* DC var. *angustifolia* (A. Gray) M. A. Lane, and *Frankenia salina* (Molina) I. M. Johnst.). High marsh areas in freshwater marshes may be particularly vulnerable to salinity shifts, as well as transitional/upland areas of other tidal marshes. These areas are of particular concern because high marsh areas contain many of the rare and endangered species that are found in California tidal marshes (Baye et al. 2000). Salinity effects have been shown to be of greater importance for vegetation zonation in low latitude marshes on the Atlantic coasts (Pennings et al. 2005), and greater impacts from salinity are likely on the Pacific Coast where Mediterranean-type climate leads to high soil salinities in salt and brackish marshes. In this regard, it could be that marshes in SF Estuary and northern California become more like those in southern California, which are predominately salt marshes with very small, localized areas of brackish and freshwater marsh.

Atwater et al. (1979) first reported that freshwater marshes of the Delta are characterized by greater plant species diversity than the salt marshes of the lower SF Estuary. As part of the Integrated Regional Wetlands Monitoring Program (IRWM, www.irwm.org), we surveyed plant distributions at six tidal marshes along a salinity gradient from the Petaluma River to the western Delta (Carl's Marsh, Pond 2A, Coon Island, Bull Island, Browns Island and Sherman Lake). Similar to Atwater et al. (1979) we found

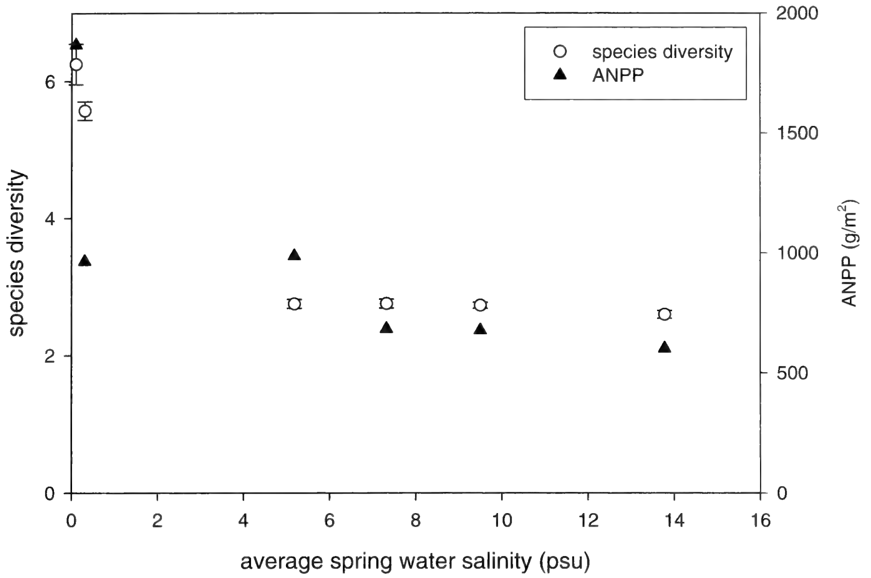

FIG. 1. Average plant species diversity per 3m-diam. plot and ANPP decrease with increasing salinity in the San Francisco Bay-Delta estuary (error bars = ±1 SE; number of random plots per site range from 151 to 447). Salinity data represent measurements averaged across spring months in 2004 (Wetlands and Water Resources unpublished data). ANPP values were derived from site-specific averages of total standing biomass of individual dominant species that were scaled up to site-level estimates using vegetation maps, and then adjusted by site area to obtain ANPP estimates at the g m^{-2} level. Sites included in order of increasing salinity are: Sherman Lake, Browns Island, Bull Island, Coon Island, Pond 2a, and Carl's Marsh.

a dramatic, non-linear increase in plant species diversity and annual net primary productivity in the fresh and brackish region of the SF Estuary (Fig. 1). Sites that are most saline have relatively low species diversity; however, even sites that are less saline in the upper part of the Napa River are not markedly more diverse. Marshes located farther east in the delta, on the other hand, are substantially more diverse and have greater numbers of locally uncommon and rare species than the four lower SF Estuary sites, including *Lilaeopsis masonii* Mathias & Constance and *Oenothera deltoides* Torr. & Frém. subsp. *howellii* (Munz) Klein. Sanderson et al. (2000) suggested that the low species numbers found at Carl's Marsh, a relatively young restored marsh, are not so much a function of marsh age as its position along the salinity gradient. Despite sampling a total of 1730 0.25-m^2 quadrats in the Petaluma Marsh, an ancient salt marsh larger than any of our sites, they only encountered a total of 14 species (Sanderson et al. 2000). The greater diversity at freshwater sites underscores the potential ecological importance of freshwater tidal marshes in the upper SF Estuary and their potential vulnerability to salt water intrusion. Given the large number of locally uncommon and rare species in the freshwater tidal marsh ecosystem, as suggested by Lyons et al. (2005) the loss of these marshes could have large consequences for ecosystem function in this region.

As salinity regimes change and plant communities shift, a substantial drop in overall vascular plant productivity is likely within tidal marshes. Increased salinity in a greenhouse experiment reduced both rates of photosynthesis and growth in *S. foliosa* and *Schoenoplectus robustus* (Pursh) M. T. Strong with a small reduction in growth only for *S. pacifica* (Pearcy and Ustin 1984). End-of-year biomass data from a range of the SF Estuary tidal marshes of differing salinity also reflect large increases in productivity with reduced salinity. Mahall and Park (1976a) estimated productivity for *S. foliosa* ranging from 270 to 690 g m^{-2}, and 550 to 960 g m^{-2} for *S. pacifica*. In comparison, Atwater et al. (1979) found end-of-year biomass ranging from 300 to 1700 g/m^2 for *S. foliosa* and 500 to 1200 g/m^2 for *S. pacifica*. Similarly, in other estuarine marsh systems, production rates are consistently lower in salt marshes (Odum 1988), likely due to the added stress of high salinities in salt marsh soils. In addition to shifts in overall productivity across our six sites along a salinity gradient (Fig. 1), we found that productivity of *S. pacifica* at three sites across the northern SF Estuary (China Camp, Pond 2a, and Coon Island) was highest in less saline locations within its distribution range (Schile, Callaway, Parker, and Vasey unpublished).

Beyond shifts in plant composition and productivity, there is some evidence that there could be outright loss of some marshes if salinity shifts

are rapid. Marsh loss due to salt water intrusion has been documented in a number of specific cases in Louisiana (Wang 1988; Day et al. 2000). Nyman et al. (1990) identified important implications of tidal marsh soil characteristics for salt water intrusion, with a much greater need for mineral sediment accumulation with increasing salinity. In order to build the same depth of soil, salt marshes required almost twice as much mineral sediment as in brackish marshes and four times that in freshwater marshes (Nyman et al. 1990). Given these requirements, as well as existing differences in soil bulk densities across salinity gradients, the substrate in freshwater marsh may not immediately support a brackish marsh if salinities increase abruptly. Increased salinity stress associated with the 2000 drought was an important factor in the large-scale die-off of salt marshes in Louisiana and Georgia; however, in both cases other factors were also critical, including likely drops in soil pH associated with drying of soils in Louisiana (McKee et al. 2004) and intense herbivory by snails in a variety of locations (Silliman et al. 2005).

Sea-level Rise and the Impacts of Inundation

Recent rates of global sea-level rise have been approximately 1–3 mm yr^{-1} over the last century (IPCC 2001). The recent report from the Intergovernmental Panel on Climate Change (IPCC) documented a global rate of 3.1 mm yr^{-1} from 1993 to 2003 compared to 1.8 mm yr^{-1} from 1961 to 1993, although it is not clear if this increase is due to normal decadal variability or a longer-term trend (IPCC 2007). The increase in sea level is due to thermal expansion of ocean waters and increased inputs of water from melting glaciers and ice sheets. A recent evaluation of tide gauge data indicates that the average rate over the 20th century was 1.7 mm yr^{-1} with an acceleration over that period of 0.013 mm yr^{-2} (Church and White 2006). If this rate of acceleration were to remain constant over the next century, it would result in sea-level rise of 28–34 cm by 2100, with an annual rate of 3–4 mm yr^{-1} by the end of the century (Church and White 2006). The IPCC has intensively evaluated future rates of global sea-level rise, using a range of emissions scenarios, and their predictions indicate a potential increase from 1990 to 2100 of 0.09 to 0.88 m across these scenarios (IPCC 2001; Fig. 2). However, these predictions have not included potential impacts from the melting of large-scale ice sheets in Greenland or Antarctica, which could increase these predictions substantially (see below). Most of the scenario predictions were in the range of 0.3 to 0.5 m over this period. Additional evaluation of model uncertainty shows a similar range of variation based on the use of different atmospheric-ocean general circulation models (11–77 mm by 2100 for a single scenario). Based on the IPCC results, it appears likely that sea level will increase approximately 15 cm by 2050, with a possible range of 5 to 30 cm (based on the 1990 baseline). Predicted increases diverge by 2100, with overall increases by that time ranging from 0.2 to 0.7 m (Fig. 2). However, recent projections of sea-level rise based on semi-empirical relationships to changes in global mean surface temperature indicate that sea-level rise could be greater than previous IPCC predictions (Rahmstorf 2007). Using the IPCC scenarios of global warming, Rahmstorf (2007) estimated potential increases in sea level ranging from 0.5 to 1.4 m by 2100.

More rapid melting of global ice sheets, primarily in Greenland and the Antarctic could lead to even greater rates of sea-level rise. Flow rates of outlet glaciers associated with the Greenland ice sheets have increased dramatically in the last decade (Rignot and Kanagaratnam 2006). Evaluation of paleoclimate records of melting and sea-level rise also indicate that future rates of both melting and sea-level rise may be much greater than current predictions (Overpeck et al. 2006). Substantial uncertainty remains concerning rates of melting for these ice sheets; however, the potential for large contributions from these sources should be considered. If these ice sheets were to melt completely, the Greenland ice sheet would contribute approximately 7 m to sea level, while the West Antarctica ice sheet would add 8 m. Globally, ice sheets could add 70 m to sea level (Alley et al. 2005). While melting at this scale is unlikely even over many centuries, it possible that melting ice sheets could increase global sea level by a meter or more over the next century (Overpeck and Cole 2006).

Increases in global sea-level rise will lead to increased rates of inundation across all intertidal ecosystems. Within any particular tidal marsh, relative sea-level rise (RSLR) is also affected by local factors that can add to or reduce the effects of global sea-level rise, including subsidence and surface sediment compaction, mineral and organic sediment accumulation, organic matter decomposition, and tectonic activity (Callaway et al. 1996; Nuttle et al. 1997). Under current conditions, most tidal marshes are relatively stable; increases in global sea level or other factors listed above are counterbalanced by sediment accumulation, and the marsh plain maintains elevations approximating mean high water (MHW) to MHHW (Redfield 1972; MacDonald 1977; Callaway et al. 1996). Any major shifts in the relative balance of these factors will lead to changes in elevation, e.g., rapid sediment accumulation from the watershed can lead to supratidal elevations and the conversion of marsh to transitional or upland habitat (Greer and Stow 2003; Callaway and Zedler 2004), while loss of

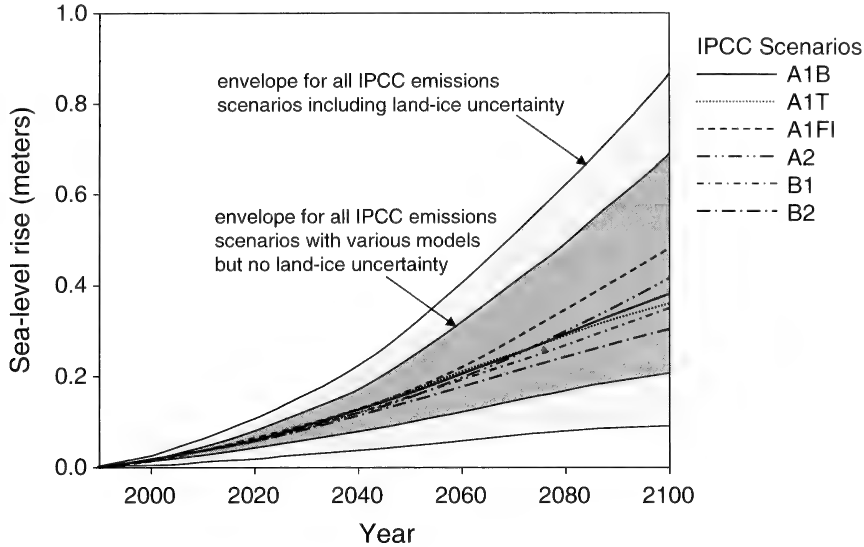

FIG. 2. Global average sea-level rise from 1990–2100, based on six scenarios from the Special Report on Emission Scenarios (SRES) from the Intergovernmental Panel on Climate Change (IPCC). See IPCC (2001) for details on scenarios. Each line represents average predictions from runs of multiple general circulation models. The region in dark shading represents the range of all general circulation models for all 35 SRES scenarios; the region in light shading represents the range of all models and scenarios including uncertainty in land-ice changes and other factors. Adapted from IPCC (2001).

elevation can lead to habitat shifts (Warren and Niering 1993; Donnelly and Bertness 2001) or loss of marsh (Baumann et al. 1984; DeLaune et al. 1994; Day et al. 1995). Tectonic activity can cause increases or decreases in relative elevation; Reed (1989) documented massive subsidence in Chile which allowed for subsequent development of a tidal marsh over a former upland forest, while uplift associated with tectonic activity has also shifted intertidal plant communities in Alaska (Thilenius 1990). High rates of local subsidence reduce relative elevation, causing increased rates of inundation and potentially marsh loss. This is occurring in a number of deltaic systems including the Mississippi River (Baumann et al. 1984; Day et al. 2000) and the Nile (Stanley and Warne 1993; Stanley and Warne 1998), and in the Chesapeake Bay (Kearney and Stevenson 1991; Ward et al. 1998). The ongoing loss of marshes in areas with high rates of local subsidence can be used as an analogy for potential widespread effects of future increased rates in global sea level, especially as the rates of subsidence in these areas (approximately 1 cm/yr) are at the high end of predictions for global sea level-rise in the next century.

Response of Marsh Vegetation to Inundation

Marsh plants have a number of adaptations that allow them to tolerate some level of inundation. Many species found along creek banks and at lower elevations, in particular *Spartina* spp., *Schoenoplectus* spp., and *Typha* spp., have well-developed aerenchyma, internal tissue with large, connected air spaces that allow for the passage of gases from plant shoots to roots (Armstrong 1979; Kludze and DeLaune 1996; Maricle and Lee 2002). Aerenchyma enables plant roots which are growing in anaerobic conditions to use oxygen from aboveground and may also result in oxygen diffusion into soils adjacent to roots and rhizomes (Howes and Teal 1994). In addition to the structural adaptation of aerenchyma, marsh plants have physiological adaptations that allow them to tolerate inundation, including shifting from aerobic to anaerobic respiration (Mendelssohn et al. 1981; Burdick and Mendelssohn 1990; Maricle et al. 2006). Despite these adaptations, marsh plants still have limits to the level of inundation that they can tolerate; as they are flooded more and more, they have less energy available for growth, and even the most tolerant plants will be subject to stresses that restrict the lower limits of their distribution.

The key questions of interest for the future stability of restored marshes are: (1) how much of an increase in sea-level rise can well-established restored marshes tolerate, and (2) will recently restored marshes be able to develop under increased rates of sea-level rise? In terms of well-established restored marshes, the range of possible outcomes is similar to those for natural marshes. They could (1) accumulate sediment in pace with increases in sea level with little change in overall vegetation; (2) undergo inundation but migrate landward towards higher elevations with local shifts towards more inundation tolerant

plant communities; or (3) be inundated quickly or have no opportunity for migration, resulting in the conversion to unvegetated mudflats. Recently restored sites will either accumulate enough sediment to build in elevation and develop as a vegetated marsh, or they will not accumulate enough sediment to reach threshold elevations for plant establishment and remain as unvegetated mudflats.

If we first consider well-established marshes, accretion and elevation data from a range of natural marshes with varying rates of local sea-level rise (due primarily to different subsidence rates) give insight into possibilities for long-term stability. Most marshes accrete sediment at a rate of 1–5 mm yr^{-1} while some may accumulate up to 10–15 mm yr^{-1} (Stevenson et al. 1986; Reed 1990; Callaway et al. 1996). Most tidal marshes appear to be relatively stable with little shift in vegetation or loss of elevation; however, some may be experiencing slight changes in elevation and resulting shifts in vegetation (Warren and Niering 1993). Donnelly and Bertness (2001) used plant macrofossils in marsh sediment cores to document that *S. alterniflora* has migrated landward in two New England marshes since the late 19th century, paralleling increases in local sea level. Some tidal marshes have much greater sediment deficits compared to marshes maintaining suitable elevations and are being converted to unvegetated mudflats (e.g., Louisiana and Chesapeake Bay, see details below). Stevenson et al. (1986) showed a strong positive correlation between local rates of RSLR and vertical accretion, indicating that marshes respond to increased rates of inundation by accumulating additional sediment. This is to be expected since areas that are lower in elevation and inundated for longer periods should have more potential for sediment accumulation (Pethick 1981; Krone 1987; French 1993; Orr et al. 2003). Availability of mineral sediments, either from local watersheds or reworked estuarine sources, will also affect rates of sediment accretion (Williams and Orr 2002). In addition, organic matter provides much of the structure for marsh sediments, and there is a strong positive relationship between organic matter accumulation rates and vertical rates of sediment accretion (Bricker-Urso et al. 1989; Nyman et al. 1990; Callaway et al. 1997). This implies a positive feedback between marsh productivity and maintenance of elevation and suggests that as marshes are subjected to increased inundation, they could hit a threshold elevation that will lead to greater plant stress and a reduction in organic matter accumulation and vertical accretion (DeLaune et al. 1994; Morris 2006).

Two well-researched examples of tidal marshes that have not been able to keep pace with RSLR include Louisiana coastal marshes associated with the Mississippi River Deltaic Plain (Baumann et al. 1984; Day et al. 2000) and brackish marshes in Nanticoke Estuary within Chesapeake Bay (Kearney and Stevenson 1991; Kearney et al. 1994; Ward et al. 1998). Many measurements of sediment accretion, subsidence, and changes in relative elevation have been completed in Louisiana using a wide variety of methods, and many of the tidal marshes in the Mississippi Deltaic Plain are not keeping pace with rates of local sea-level rise (DeLaune et al. 1978; DeLaune et al. 1983; Hatton et al. 1983; Baumann et al. 1984; Nyman et al. 1990; Boesch et al. 1994; Day et al. 2000; Turner 2001), while Gulf Coast marshes in more stable areas outside the delta, such as the Chenier Plain, and the Texas and Mississippi coastlines are keeping pace (Callaway et al. 1997). The Louisiana marshes appear to be able to withstand RSLR of up to 10 or 12 mm yr^{-1}, but at higher rates of RSLR they become submerged. In the Chesapeake Bay case, accretion rates were up to 7.4 mm yr^{-1}; however, local subsidence was very high, and marshes were not able to keep pace with sea-level rise. A number of other coastal marshes have reported marsh loss, although causes may vary. Elkhorn Slough has lost substantial salt marsh area over the last five decades, although exact causes are unclear, and loss here is more likely due to increased tidal currents and reduced sediment inputs rather than increases in sea-level rise (Van Dyke and Wasson 2005).

In addition to empirical data from natural marshes, modeling studies can provide some insight into what rates of sea-level rise are sustainable for tidal marshes. Morris et al. (2002) evaluated effects of sea-level rise on South Carolina tidal marshes using a model developed to evaluate marsh stability. Model results indicated that with relatively high rates of sediment loading as are found in this area, the marsh would be stable up to a rate of sea-level rise of 12 mm/yr. Rates higher than this led to marsh submergence and loss of vegetation. The modeled marsh had a slightly smaller tidal range (1.4 m mean tidal range) than found in San Francisco Bay. Morris et al. (2002) also found that the most stable area of the marsh was the marsh plain, even though the most productive part of the marsh was the low marsh. Orr et al. (2003) developed a model for SF Estuary marshes using the approach of Krone (1987) and French (1993). Their model tested rates of sea-level rise of 1, 3, 5, 6, and 11 mm/yr and indicated that high elevation marshes would be stable at rates of 6 mm yr^{-1} or below; low marshes were more vulnerable to increased rates, similar to Morris et al. (2002). Shifts in suspended sediment concentrations had a substantial effect on accretion rates and marsh stability. From empirical data, Orr et al. (2003) also concluded that freshwater marshes would be less affected by increases in sea-level rise

and reduced inputs of mineral sediments as they are able to accumulate organic sediments at a higher rate than salt or brackish marshes. In summary, data from natural marshes and simulation models both indicate that inundation rates on the order of 10–15 mm yr^{-1} will lead to marsh loss for well-established marshes, while rates lower than this but greater than current rates could lead to shifts in plant communities.

Implications of Inundation for Restoration

Newly restored tidal marshes are likely to be even more sensitive to increased rates of sea-level rise for a variety of reasons. First, restored marshes need to increase elevation, not just maintain elevation, in order to reach threshold elevations for plant establishment. As outlined above, many current tidal restoration projects are designed at elevations 20–50 cm below target elevations for marsh vegetation (Philip Williams and Associates Ltd. and Faber 2004). While leaving sites at low elevations and allowing natural sediment accumulation to occur has substantial benefits, this approach creates an instant sediment need for restored marshes that could make them more vulnerable to increased rates of sea-level rise, especially because low marsh areas appear to be more vulnerable to sea-level rise than high marsh areas. In addition, some restoration sites may be at even lower initial elevations, due to locally high rates of subsidence rates, organic matter oxidation, and the lack of sediment inputs when sites are behind levees. This is particularly important within south San Francisco Bay, where salt pond restoration sites have subsided anywhere from 50 to 200 cm. Areas in the Sacramento-San Joaquin Delta may be at even lower intertidal elevations (Mount and Twiss 2005).

Second, sparse vegetation (or lack of vegetation) will reduce sediment accumulation rates in restored sites. In tidal marshes, the presence of vegetation slows down tidal currents and promotes sediment accumulation (Temmerman et al. 2005). While the presence of vegetation may not be critical at low mudflat elevations, as mudflats build up to higher elevations, vegetation promotes sediment accumulation (and prevents wind waves and sediment erosion). If vegetation does not establish quickly within restored marshes, this could further limit sediment accretion rates and reduce the ability of restored marshes to keep pace with increased rates of sea-level rise.

Finally, many restored tidal marshes, especially those in urban areas, lack adjacent uplands for possible migration. In cases where there are gradual transitions to adjacent uplands, marshes may migrate inland with increases in sea-level rise (e.g., Warren and Niering 1993; Donnelly and Bertness 2001). Substantial research in the 1980's evaluated opportunities for marsh migration from a policy perspective, and in coastal areas with very shallow slopes and where infrastructure has not been established in adjacent transitional areas, there are opportunities to allow marshes to migrate upslope in the face of higher rates of sea-level rise (Titus 1990, 1991). This approach has been called managed realignment in the U.K. and has been widely promoted there (Pethick 2001, 2002). However, in most cases within California, this type of marsh migration will not be possible because of either naturally sharp topographic breaks between marshes and adjacent uplands or, more commonly, loss and/or degradation of transitional upland areas due to substantial urban, residential, industrial, or agricultural development. Because of their association with mitigation impacts and for a variety of other reasons, restored marshes often lack natural transitional habitats. If restored marshes are surrounded by urban development, dikes or other impacted areas, they will not be able to migrate inland, and increased rates of sea-level rise will lead to marsh loss.

Conclusions and Recommendations

Climate change will have substantial effects on tidal marshes in the SF Estuary and across the Pacific Coast. Initial impacts are likely to be caused by salinity changes as a result of altered flow regimes, with even relatively small salinity changes potentially causing shifts in dominant vegetation. Although tidal marsh restoration projects in general will be adversely affected by increasing salinity, tidal freshwater marshes will be the most vulnerable. They are likely to be converted to brackish marshes, with existing brackish marshes converted to salt marsh communities. These shifts will cause a loss in overall tidal marsh plant diversity and a reduction in vascular plant productivity, changes that will cascade into the associated estuarine food webs

While the impacts of inundation associated with sea-level rise may be slower to affect tidal marshes, sea-level rise could ultimately have a much more profound cumulative impact due to the combined effects of excessive inundation and more persistent changes in salinity. Low rates of predicted sea-level rise will cause shifts from marsh-plain to low-marsh vegetation, while rates at the high end of predictions could cause widespread loss of tidal marsh habitats, especially if ice sheets on Greenland and west Antarctica begin melting at a more rapid rate. In addition, the impacts of climate change are not likely to affect tidal marshes uniformly across large scales. Along the Pacific Coast, from Washington to southern California, inundation and anaerobiosis are likely to play a larger role to the north, while increases in salinity, especially in the marsh plain,

TABLE 1. SUMMARY OF TIDAL MARSH RESPONSES TO POTENTIAL SEA-LEVEL RISE CONDITIONS.

Scenario	Cumulative sea-level rise by 2100 (cm)	Annual rate of sea-level rise (mm/yr)	Marsh dynamics
Historic conditions	10–20	1–2	• restored marshes develop • natural marshes keep pace
IPCC mid-range estimates	30–50	4–6	• restored marshes slower to develop • some shift in vegetation
IPCC high-range estimates	60–90	7–10	• restored marshes unlikely to develop • large-scale shifts in vegetation • likely marsh loss
Recent high estimates	>1 m	>10	• substantial loss of both natural and restored marshes

will constrain marshes in the south. Consequently, restoration ecologists will need to consider factors such as local and regional climate variables, potential shifts in summer rainfall, and how watersheds are likely to change under different climate scenarios.

In terms of management opportunities, water management will be critical for potential salinity shifts; however, opportunities will be constrained by growing human water needs as well as the magnitude of seasonal shifts in runoff. In dealing with increases in future sea level, the greatest opportunity for preserving both natural and restored marshes will be to allow for landward migration of tidal marshes. However, as with water management, there are substantial socioeconomic constraints to dealing with adjacent land use. Purchasing areas adjacent to marshes to permit migration, rather than constructing new marshes directly will be an important component of future marsh restoration and mitigation. This also may require grading and restoration of these adjacent uplands to make the landward sites suitable for future marsh migration. On a broader scale, there is the need to identify opportunities for regional restoration/conservation of sites that will maximize preservation of tidal marsh plant diversity, in particular for tidal freshwater sites that are likely to be impacted by shifts in estuarine salinity. In considering impacts of marsh shifts on animals, the relative importance of various tidal marsh habitats for fish, birds and other target species of interest should be evaluated. Finally, sediment accumulation is a critical issue for marsh stability, and sediment within the estuary sediment should be managed as a valuable resource. Opportunities for building marsh elevation with sediment reuse should be evaluated, as well as other management activities such as small-scale sediment fences which could maximize sediment retention within restored tidal marshes.

Given these challenges and future uncertainties, it is critical that knowledge of potential impacts from current climate change models be incorporated into strategies for the design, implementation, and adaptive management of tidal marsh ecosystems. As emphasized by Millar and Brubaker (2006) and Watson (2004) for the SF Estuary, paleohistoric patterns reveal that the SF Estuary has been extraordinarily dynamic, and it is highly unlikely that the estuary will return to target conditions from the mid 19th century. Rather, we need to adopt a flexible and adaptive approach to tidal marsh restoration in the SF Estuary that will focus more on on-going adjustment to future conditions, opportunities, and trajectories. The SF Estuary is a resource of global importance and a cornerstone to the identity of the Bay-Delta Community. Accordingly, investment in its ecological recovery through marsh restoration is both appropriate and wise. However, to insure that this investment realizes its full potential, the conservation and restoration community must take climate change issues to heart and begin the task of working together in conjunction with the broader society to forge institutions capable of a more nimble response to this challenge.

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RESTORING NATIVE GRASSES AS VEGETATIVE BUFFERS IN A COASTAL CALIFORNIA AGRICULTURAL LANDSCAPE

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ABSTRACT

We investigated changes in vegetation composition of different grass buffer strips in a fragmented coastal agricultural landscape to evaluate the potential for native grass restoration of sites that receive agricultural runoff. Vegetative buffers bordering Elkhorn Slough, draining into Monterey Bay, California, were either seeded with a non-native annual grass (*Hordeum vulgare*) or with a mix of native perennial grasses (*Bromus carinatus*, *Deschampsia cespitosa*, *Nassella pulchra*), and aboveground biomass and cover of vegetation were measured over a 4-yr period. Based on preliminary results, we initiated a second, smaller-scale experiment to test establishment of native perennial grasses (*Bromus carinatus*, *Elymus glaucus*, *Hordeum brachyantherum*) at different seeding densities with combinations of non-native annual grasses (*H. vulgare* or *Lolium multiflorum* and *Vulpia myuros*) to optimize erosion control.

In the first experiment, plots seeded with non-native annual grasses had greater biomass than native perennial plots in the first year. Biomass and cover of seeded annual grass decreased each year, which resulted in these plots being dominated by unseeded non-native species by the third year. In contrast, seeded native perennial grasses increased in both biomass and cover by the second year, with little cover of non-native species; but, in the third year cover of non-native species increased. By the fourth year, unseeded non-native species provided nearly all plant biomass and cover in all treatments. In the second experiment, native perennial grass cover was low, but was greater when seeded alone compared to when seeded with non-native annuals. The seeded annual grass *V. myuros* invaded and provided the majority of cover in most plots by the second year. Our results suggest that some species of native perennial grass can establish on former agricultural lands, but long-term survival is difficult without extensive management.

Key Words: *Bromus carinatus*, *Deschampsia cespitosa*, exotic invasion, *Nassella pulchra*, native grass restoration, vegetative buffer strips.

Restoring native grasslands in California has become a conservation priority (Bugg et al. 1997; Hatch et al. 1999; Corbin et al. 2004). In a recent review, Hoekstra et al. (2005) identify temperate grasslands and Mediterranean ecosystems, as the two most threatened biomes globally, where habitat area converted to human uses is more than eight times the area protected. The remaining grasslands in California are dominated by non-native annual species from other regions with similar climatic conditions (Bartolome et al. 1986; Huenneke 1989; Corbin et al. 2004). Along the California coast, potential sites for grassland restoration are limited and are often embedded in a matrix of agricultural lands.

Increasingly restoration efforts are motivated not only by efforts to conserve biodiversity, but also to provide ecosystem services, such as erosion control and water purification (Holl and Howarth 2000; Aronson et al. 2007). Determining whether restoration projects can meet these multiple targets is critical, particularly as funding is often linked to demonstrating benefits to humans through valued ecosystem services (Holl and Howarth 2000). An example of restoration projects potentially meeting multiple goals is restoration of vegetative buffer strips (VBS), which are strips of land between agricultural lands and nearby waterways.

Past research has demonstrated that VBS improve water quality in many temperate agricultural landscapes, by removing excess nitrogen and suspended sediments from agricultural runoff before they enter surface waters (Schlosser and Karr 1981; Dillaha et al. 1989; Muscutt et al. 1993; Daniels and Gilliam 1996). However, there has been little study of restoring native species in buffer strips, particularly in Mediterranean climates, where rainfall is highly episodic.

Native grass restoration on sites receiving high nutrient input from agricultural lands may prove to be particularly challenging. Many studies have shown that nutrient enrichment, specifically N, alters competitive interactions between species and results in increased productivity, favoring intro-

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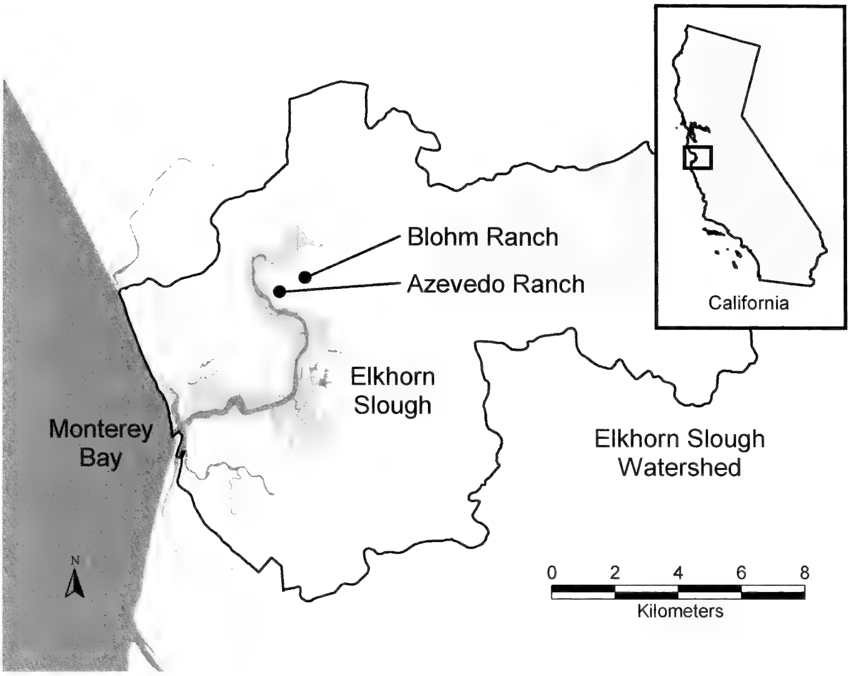

FIG. 1. Regional map of study area showing watershed boundary and study sites.

duced annual grasses (e.g., Inouye and Tilman 1995; Dyer and Rice 1997; Jeffries and Maron 1997; Hooper and Vitousek 1998; Weiss 1999).

Through two studies, we investigated the feasibility of restoring native grasses in vegetative buffer strips receiving runoff from conventional row crops along the central coast of California. At the first site, we compared plots seeded with native perennial grasses and plots seeded with a non-native annual grass commonly used for erosion control. At the second site, we evaluated if different seeding mixes and densities of native perennial grasses and non-native annual grasses could provide both short- and longer-term cover.

METHODS

Study Sites

This study was conducted in the Elkhorn Slough watershed, a major coastal wetland draining into the Monterey Bay National Marine Sanctuary (Fig. 1). The surrounding uplands have steep slopes and sandy loam topsoil, and are particularly susceptible to erosion (USDA 1984). Approximately 26% of the watershed is in agricultural production (USDA 1994). High sediment and N concentrations in agricultural runoff enter and degrade the estuary (USDA 1984; Rein 1999a; Caffrey 2002). Non-native vegetative buffers have been recommended for erosion control (USDA 1984, 1994).

The first study was conducted adjacent to and downslope from row crops on Azevedo Ranch in the Elkhorn Slough watershed (Fig. 1). The study was conducted on a 1.2 ha portion of the ranch with a slope ranging from 12–22%. At the top of the slope is a flat upper terrace, where farm activities continued. This slope drains into a salt marsh connected to Elkhorn Slough. Prior to the study, strawberries were grown on both the slope and the terrace, with rows extending to the edge of the marsh. Beginning in July 1995, crop production was limited to the terrace, and the 1.2-ha slope was used for this study. The Azevedo study was conducted over the following period: September 1995–September 1996 (first year), 1996–1997 (second year), 1997–1998 (third year) and 1998–1999 (fourth year). The years correspond to agricultural and rainfall years, rather than calendar years. During these four years, strawberries were grown in the first year and flowers (*Delphinium* sp.) cultivated in the second, third, and fourth years.

A second experiment was established in September 1997 (the third year of the Azevedo study) at Blohm Ranch, which is located approximately 1 km up-slope from Azevedo Ranch (Fig. 1). Blohm Ranch was taken out of agricultural production in 1996; therefore only residual agricultural fertilizers rather than an ongoing input contributed to surface and subsurface runoff during the study period. The site has an average slope gradient of 20–25%.

The soils on both the study sites are Arnold loamy sand and Elkhorn fine sand (USDA 1979). Soils (0–15 cm) were 11–20% clay, 7–25% silt,

64–73% sand, and dry bulk density was 1.2 g cm^{-3}. Although classified as similar soils, the Azevedo soils are finer textured than the loamy sands of the Arnold series on the Blohm ranch. There is a shallow clay horizon located within 50 cm from the surface at Blohm Ranch, while Azevedo has a deeper clay layer ranging from 1–6 m below the surface.

The local Mediterranean climate is characterized by an extended dry season (May–September) and episodic rain storm events primarily between November and April. Rainfall varied substantially among the years of the study in both total quantity and intensity, with annual rainfall above the 20-yr average for the watershed (450 mm) in all years of the study (USDA 1994). Annual rainfall ranged from 587 mm yr^{-1} to 761 mm yr^{-1} during the study period and was highest in the El Niño year of 1997–1998, as measured at a California Irrigation and Management Information Station 7 km from the study area (DWR 2005).

Azevedo Ranch Experimental Design

Six plots (40 m × 20–39 m) were created along the topographic fall line. The plots were located down-slope from and received surface and subsurface water flow from the row-crop agriculture. Each plot was assigned to one of two treatments in a randomized complete block design: (1) native perennial grasses (a mix of *Bromus carinatus* (California brome), *Deschampsia cespitosa* (tufted hairgrass), and *Nassella pulchra* (purple needlegrass); or (2) non-native annual grass, 100% *Hordeum vulgare* (common barley). Nomenclature follows Hickman (1993), and a full species list is available from the authors. Perennial grass seeds were purchased from the Elkhorn Native Plant Nursery (Moss Landing, CA), with seeds collected within the watershed. *Hordeum vulgare* was selected because it is used as a cover crop and to control erosion; seed was purchased from General Feed and Seed (Santa Cruz, CA). Unseeded plants in all plots established from seeds dispersed from adjacent lands and the seed bank.

Azevedo Ranch Site Management

At Azevedo Ranch, the soil was disked in September 1995, and then irrigated. Emergent weeds were disked in once, prior to seeding the plots in October 1995, in an effort to reduce the weed seed bank. Grass seeds were hand broadcast and buried by disking to a depth of 15–20 cm, and irrigated once in November 1995 to increase seed germination before the onset of rains. Seeding rates were *N. pulchra*—85 seeds m^{-2}, *B. carinatus*—210 seeds m^{-2}, *D. cespitosa*—1000 seeds m^{-2} and *H. vulgare*—600 seeds m^{-2}, based on recommended rates for disking seeds in for erosion control (P. Kephart, Director, Rana Creek Ranch).

Non-native annual grass plots were re-seeded by hand broadcasting in November 1996 and October 1997 to ensure re-establishment. Non-native annual grass plots were mowed to a height of 10–15 cm after *H. vulgare* senescence in June 1996 and May 1997, pursuant to the farmer's concern about birds perching on the grass stalks and consuming strawberries.

Azevedo Ranch Vegetation Sampling

In February 1996, February 1997, April 1997, April 1998, and May 1999, species composition, percent cover and above-ground biomass were measured in three 30 × 30 cm quadrats randomly located along three transects at 5, 20, and 40 m from the upper plot boundary (9 quadrats total). In the final year, cover was recorded in six quadrats (two per transect) and biomass was only recorded in two quadrats, as there were few to no target species in the plots.

Cover was estimated visually to the nearest percent (Dethier et al. 1993). Above-ground biomass was clipped, dried at 60°C, and weighed to the nearest 0.1 g. Harvested plants were separated into two groups: species seeded in a plot (*H. vulgare* or native perennial grass) and non-seeded species (including species that were seeded in another treatment and spread).

Blohm Ranch Experimental Design

The treatment area was subdivided into four blocks, each with seven 5 × 5 m plots. Each plot was assigned to one of seven treatments with different seeding densities of three seed mixes: (1) native perennial mix (*Bromus carinatus*, *Elymus glaucus* (blue wildrye) and *Hordeum brachyantherum* (meadow barley)); (2) *Hordeum vulgare*; and (3) *Lolium multiflorum* (Italian ryegrass) and *Vulpia myuros* (Zorro fescue). The seven treatments (Table 1) included seeding each species mix individually, as well as seeding 50% and 75% proportions of the two non-native annual mixes with 50% and 25% native perennials to determine if the annuals would provide short-term cover while allowing for long-term establishment of native perennial grasses.

Species and seeding rates (Table 1) were selected based on results of the initial study, local plant experts, typical erosion control practices, and site-specific conditions (J. Fodor, Central Coast Wilds, and P. Kephart, Rana Creek Ranch, personal communications). At the time of the study, the National Resource Conservation Services (NRCS) widely recommended a mix of *L. multiflorum* and *V. myuros* for erosion control in this region (R. Caselle and D. Mountjoy, NRCS personal communication). *H. vulgare* was

TABLE 1. SEEDING TREATMENTS AT BLOHM RANCH.

Treatment name	Composition	Seeding Rate (kg/h)[1]
Native perennial grass mix (Per)	33% *Elymus glaucus*	3
	33% *Hordeum brachyantherum*	3
	33% *Bromus carinatus*	3
Hordeum vulgare (Hv)	100% *Hordeum vulgare*	43
Lolium multiflorium/Vulpia myuros (Lm/Vm)	50% *Lolium multiflorum*	3
	50% *Vulpia myuros*	3
High density perennial with *H. vulgare* (Per-High-*Hv*)	50% *H. vulgare*	21.5
	50% native perennial grass mix	1.5 (each)
High density perennial with *L. multiflorum/V. myuros* (Per-High-*Lm/Vm*)	50% *L. multiflorum/ V. myuros*	1.5 (each)
	50% native perennial grass mix	1.5 (each)
Low density perennial with *H. vulgare* (Per-Low-*Hv*)	75% *H. vulgare*	32.3
	25% native perennial grass mix	0.75 (each)
Low density perennial with *L. multiflorum/V. myuros* (Per-Low-*Lm/Vm*)	75% *L. multiflorum/ V. myuros*	2.25 (each)
	25% native perennial grass mix	0.75 (each)

[1] Differences in seeding rates reflected differences in seed weight.

selected because farmers commonly use it as a cover crop, and it established rapidly in the main study. All seeds, except *H. brachyantherum*, were provided by the NRCS. *H. brachyantherum* seeds were purchased from Central Coast Wilds (Santa Cruz, CA).

The soil was disked and level planed in September 1997. Grass seeds were hand broadcast and buried by disking. A 1-m strip between plots was seeded with *V. myuros*. The field surrounding the study plots was hydroseeded by the land manager with an erosion control mix consisting of *B. carinatus*, *H. vulgare*, *Trifolium hirtum*, and *V. myuros*.

Blohm Ranch Vegetation Sampling

Plant cover and biomass were measured at Blohm Ranch using the same procedures as at Azevedo Ranch. Vegetation cover and biomass were sampled in one 30 × 30 cm quadrat per plot; quadrats clipped in the previous year were not resampled. Vegetation was sampled in April 1998 and May 1999, the first and second years after seeding. Harvested plants were separated into seeded species (Table 1) and volunteers (species not seeded) for biomass measurements.

Statistical Analyses

We analyzed all data using SAS software version 8.1 (SAS Institute, Inc., Cary, NC). Biomass and cover data were analyzed using a t-test for Azevedo and a one-way ANOVA for Blohm with vegetation treatment as the independent variable, and data from each year analyzed separately. Data were log-transformed (biomass) or arcsin-transformed (cover) when necessary. The multiple vegetation quadrats per plot at Azevedo were averaged prior to statistical analysis. If treatment was found to be significant in the ANOVA, then Tukey's multiple comparison procedure was used to test differences between treatments.

RESULTS

Azevedo Ranch

In the first year, biomass of the native perennial grass mix was lower than in the annual grass treatment (Fig. 2A; $t = 5.0$, $P = 0.007$). By the second year, however, native perennial grass biomass was significantly greater than the annual grass treatment (Feb.: $t = 9.2$, $P < 0.001$, Apr.: $t = 4.1$, $P = 0.015$). Cover of seeded species in the first two years showed similar trends to biomass, except that unseeded species had higher relative cover than biomass, resulting in no significant treatment differences in total cover (Fig. 2B; $t < 2.0$; $P >> 0.05$ in all cases). In the third year, native perennial grasses remained dominant but *H. vulgare* did not re-establish well, and both cover and biomass in the annual grass treatment was dominated by unseeded species (Fig. 2). By year four, nearly all cover in both treatments was comprised of unseeded species with no difference in cover ($t = 2.6$, $P = 0.234$). Similarly, biomass was 99% unseeded species.

Of the three native perennial grass species seeded, *B. carinatus* comprised >90% of native perennial grass cover with <5% cover of the other two species. None of the seeded species established substantially outside their seeded area. Cover of the few species of native volunteers, such as *Anaphalis margaritacea*, *Lotus scoparius*, and *Lupinus bicolor*, totaled less than 5% in any given year. The relative abundance of non-native volunteers changed over time. Averaged across all treatments, *Poa annua* (6%) and the annual forbs *Erodium botrys* (9%) and *Trifolium hirtum* (6%) were the most abundant in the first year, but their cover decreased in subsequent

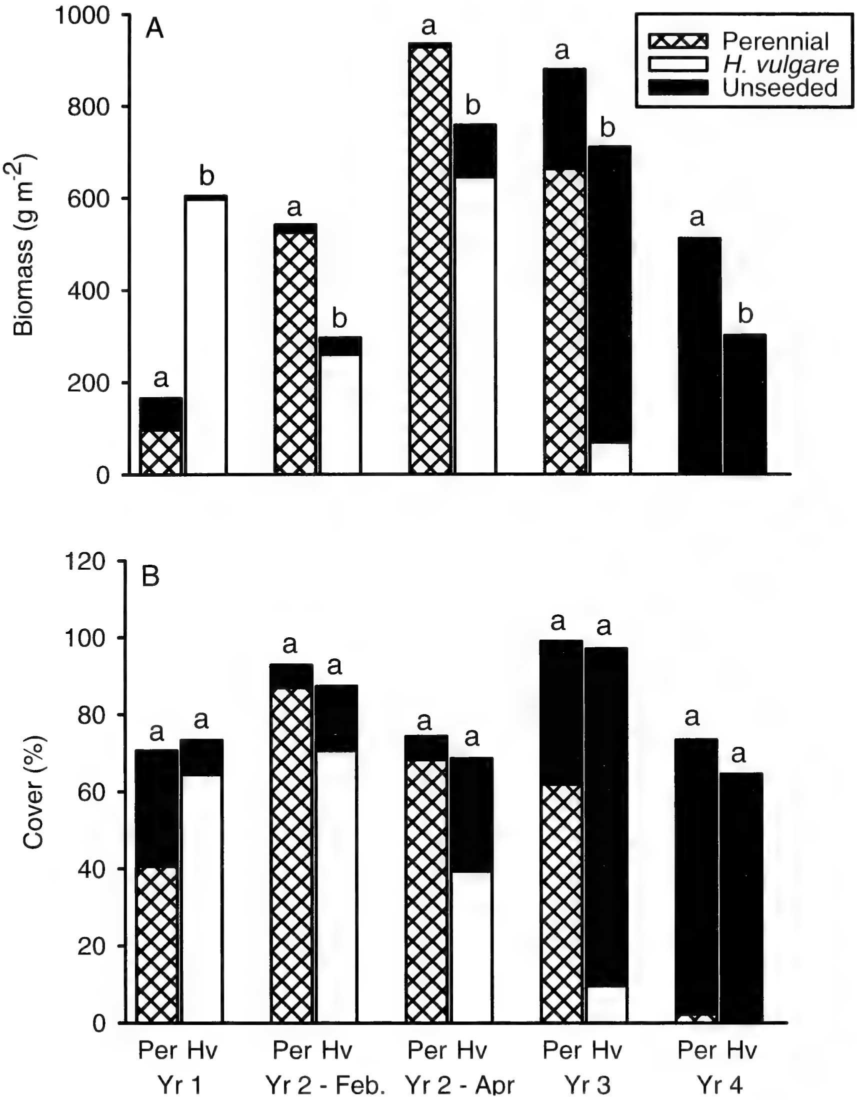

FIG. 2. Vegetation biomass (A) and cover (B) in perennial grass (P) or annual grass *Hordeum vulgare* (*Hv*) treatments at Azevedo Ranch over four years. Shading indicates composition of vegetation: seeded native perennial grasses, seeded exotic annual *H. vulgare*, or unseeded, volunteer species. n = 3 for all treatments. Treatments with the same letter do not have significantly different total biomass or cover.

years. The N-fixer, *Medicago polymorpha*, had high cover in the second (10%) and third (32%) years. Non-native plants in the Asteraceae family (*Picris echioides*, *Conyza canadensis*, and *Senecio* sp.) established in the first year and became increasingly important over time. By the third year, these species, along with *Epilobium* spp., were dominant. Several grass species, such as *Vulpia myuros* (15%) and *Lolium multiflorum* (9%), replaced the forbs by the fourth year.

Blohm Ranch

Native perennial grass cover at Blohm Ranch was low in both years compared to Azevedo, but was significantly greater in plots seeded with 100% native perennial grasses (Fig. 3B; 1998: $F = 3.7$, $P = 0.012$; 1999: $F = 16.1$, $P < 0.001$). In the first year, total biomass and cover, comprised primarily by unseeded species, in particular *Medicago polymorpha*, were similarly high across treatments (Fig. 3; $F < 1$, $P >> 0.05$ in both cases). By the second year, *V. myuros*, and a much smaller amount of *L. multiflorum*, comprised a similarly large percentage of the cover in all treatments (27–57%; Fig. 3; $F = 0.88$, $P = 0.529$), whereas cover of *H. vulgare* was nearly non-existent (<1%). In year 2, total biomass was considerably lower due to reduced biomass of unseeded species. Again, total biomass and cover did not differ significantly by treatment (Fig. 3; $F < 1$, $P >> 0.05$ in all cases).

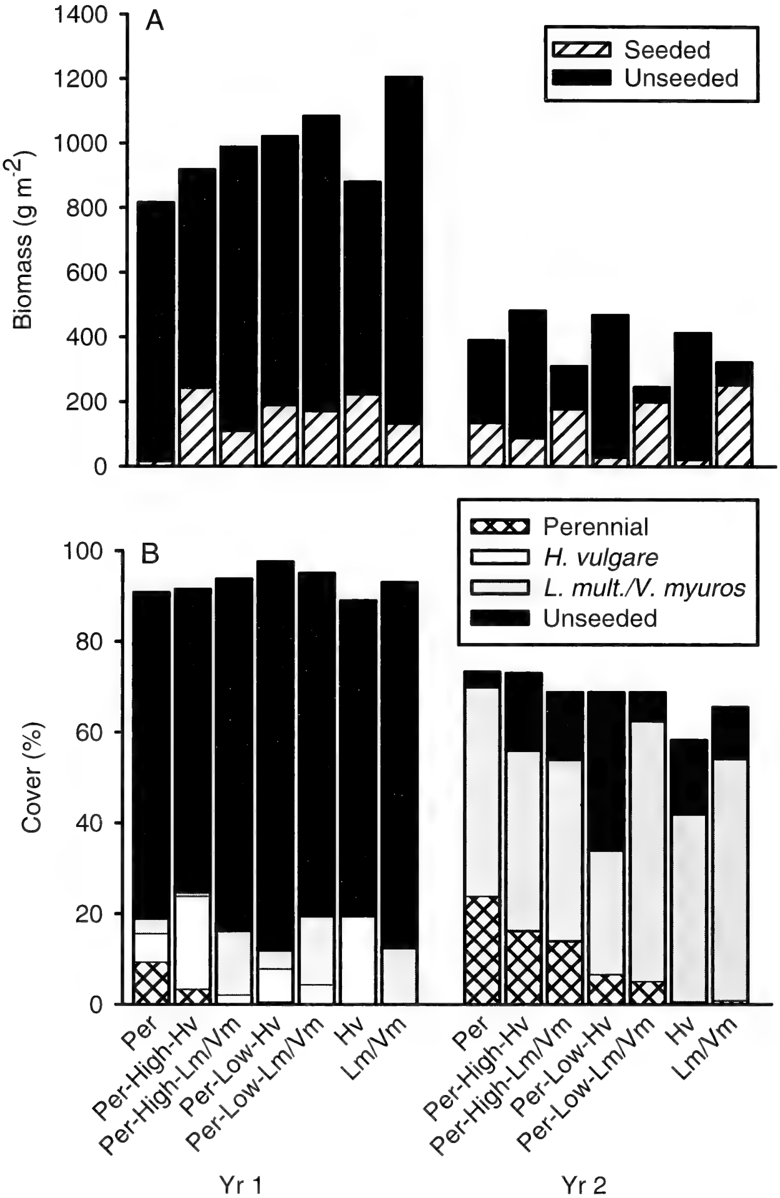

FIG. 3. Vegetation biomass (A) and cover (B) at Blohm Ranch. Shading indicates vegetation composition. See Table 1 for full treatment descriptions. Biomass is separated into species that were seeded into a specific treatment (seeded) and those which were not seeded into that treatment (unseeded). Cover was separated into native perennial grasses (perennial), *Hordeum vulgare* (*Hv*), *Lolium multiflorum* and *Vulpia myuros* (*Lm*/*Vm*), and species not seeded into a treatment (unseeded).

Of the native perennial grasses, *H. brachyantherum* had the highest proportion of cover (63%) with substantial cover of *B. carinatus* (30%) and lower cover of *Elymus glaucus* (7%). Like at Azevedo, cover of native volunteers was less than 5%. In the first year, most plots were colonized by *Medicago polymorpha* (51%) and *Trifolium hirtum* (19%); by the second year, however, each of these species covered less than one percent averaged across all plots. In 1999, the same non-native Asteraceae as at Azevedo (2%), the annual non-native forb *Erodium botrys* (4%), and the native *Lotus scoparius* (3%) were among the most abundant.

DISCUSSION

The goal of this research was to determine the feasibility of restoring native perennial grasses in vegetative buffer strips in an agricultural landscape in coastal California, while simultaneously providing sufficient cover to minimize erosion

and prevent agricultural sediments from entering into nearby water bodies. The results of our two studies indicate that: 1) perennials do not establish rapidly in the first year which makes the sites vulnerable to initial erosion and non-native invasion; 2) perennials establish higher cover by the second year; 3) perennial grasses can establish when seeded in combination with annuals, but their cover is lower and some common erosion control species (e.g., *Vulpia myuros*) may themselves be invasive; and 4) over the long-term it will be challenging to maintain perennial grasses in sites with high nutrient and non-native seeds inputs without extensive ongoing management.

Vegetation Establishment

The potential to use areas adjacent to agriculture to restore native habitat and effectively reduce agricultural sources of pollution in a Mediterranean climate depends on the rapid establishment of vegetative cover. In both our experiments, the seeded non-native annuals established more dense cover and biomass in the first year than the native perennial grasses. This result is consistent with other restoration projects and studies comparing annual and perennial plant growth rates (e.g., Anderson 1993; Garnier and Vancaeyzeele 1994; Corbin and D'Antonio 2004), particularly in high nutrient environments (Classen and Marler 1998).

By the second year, perennial grass biomass was more than five times higher at both sites and provided a similar amount of erosion control as the annual treatment at Azevedo (Rein 1999b). Our results, as well as several other studies in California, show that native perennial grasses can successfully establish in an agricultural environment (Anderson 1993; Stromberg and Kephart 1996; Bugg et al. 1997; Seabloom et al. 2003; Corbin and D'Antonio 2004).

At both sites, *Bromus carinatus* established well, and *Hordeum brachyantherum* provided substantial cover at Blohm Ranch. *Deschampsia cespitosa* comprised less than 5% of the native perennial cover throughout the study at Azevedo. *D. cespitosa* has small seeds and may have been buried too deeply when initially disked in, accounting for the low establishment success. *Nassella pulchra* also had low cover, although it has been successfully reintroduced in other restoration studies (Corbin and D'Antonio 2004; Fehmi et al. 2004). It may not have established well since it is sensitive to low light levels and may have been shaded out by *B. carinatus* (Dyer and Rice 1997, 1999). Stromberg and Kephart (1996) similarly note that *B. carinatus* had much higher cover than *N. pulchra* in the first few years in other restoration projects in the region.

Seeding Mixes of Annual and Perennial Grasses

It is difficult to conclude whether mixed seeding of non-invasive annual grasses, such as *H. vulgare*, and perennial grasses is a suitable strategy for restoring native grasses and providing erosion control, given that overall establishment of both annual and perennial grasses was quite low in all treatments, compared to at Azevedo. This lower establishment likely resulted from a number of factors. First, less effort was made at Blohm Ranch to exhaust the weed seed bank and the plots were much smaller, likely increasing the abundance of unseeded species, in the first year. Second, the hardpan at Blohm Ranch created a different moisture regime than at Azevedo. Third, Blohm ranch was not irrigated prior to the rainy season so some seed may have washed off in early storms. Fourth, nearby agricultural activities had ceased by the time of the study at Blohm Ranch, so ongoing inputs of N were likely substantially lower than at Azevedo. These different results highlight the importance of testing restoration treatments at multiple sites before making general management recommendations and tailoring restoration strategies to site conditions (Anderson 1993; Stromberg and Kephart 1996).

Results from the Blohm Ranch study concur with previous research showing that *V. myuros* is highly invasive and may suppress perennial grasses (Brown and Rice 2000); therefore, its use in proximity to native grass restoration projects is not advisable. In our study at Azevedo, none of the native perennial grasses nor the *H. vulgare* established noticeably outside their seeded area. In contrast, at Blohm Ranch, *V. myuros* spread across the entire test site. A total of five species was included in the mix drill-seeded across the surrounding areas, yet only *V. myuros* dominated the site by the second year (Rein personal observation).

Resisting Invasion

Restoring native grasslands requires not only initial establishment of native species, but also the ability to resist invasion by non-native plant species over the long-term. After the second year at Azevedo native grass restoration appeared successful, yet by the fourth year there were few native perennial grasses remaining. Restoration projects often are evaluated after two or three years and monitoring may not continue. In restoration sites, species composition is often dynamic, especially on post-agricultural land (Inouye and Tilman 1995; Muller et al. 1998), necessitating the need for ongoing monitoring and management (Anderson 1993; Stromberg and Kephart 1996).

Due to the high nutrient input from agricultural runoff at Azevedo, it is not surprising that

the non-natives invaded all treatments. Nutrient enrichment usually favors non-native species, including annual grasses (D'Antonio and Vitousek 1992; Inouye and Tilman 1995; Jeffries and Maron 1997; Hooper and Vitousek 1998; but see Seabloom et al. 2003; Thomsen et al. 2006). Furthermore, as vegetative buffers occur in fragmented and often disturbed habitats, non-native seed sources are abundant.

Although many studies have shown that perennial grasses in California are limited by competition with non-native species (e.g., Dyer and Rice 1997, 1999; Fehmi et al. 2004; Buisson et al. 2006), some studies have found that the native perennial grasses are able to outcompete non-natives over time (Corbin and D'Antonio 2004) and even reinvade annual grass stands if seeded (Seabloom et al. 2003). These contrasting results are probably due to a variation of past agricultural history, soil nutrients, non-native control efforts, and species studied (Anderson 1993; Stromberg and Griffin 1996; Seabloom et al. 2003). In particular, we made substantially less effort to control non-native species prior to and during the experiment than restoration practitioners recommend (Anderson 1993; Stromberg and Kephart 1996), in part due to concerns about using herbicides immediately adjacent to a National Estuarine Research Reserve.

The dominant native species in the Azevedo study *Bromus carinatus*, has received relatively little study compared to *Nassella pulchra*. Seabloom et al. (2005) likewise showed that it decreases in cover within a few years after seeding, which may be one reason for the low resistance of our restoration treatment to invasion. Differences in responses among perennial grass species, highlight the problems with generalizing conclusions about vegetation dynamics of all native grasses based on studies of one or two species, as species may respond quite differently to varying site conditions and disturbance regimes (Bugg et al. 1997; Hayes and Holl 2003; Bartolome et al. 2004; Thomsen et al. 2006). In particular, the vast majority of past grassland restoration in California has been done on inland grasslands and the results of coastal studies are often quite different (Corbin and D'Antonio 2004).

In conclusion, restoring native grasslands in a highly fragmented agricultural landscape with ongoing nutrient inputs and extensive non-native seed sources will be challenging and resource intensive. It will require careful species selection and further testing over multiple years to determine whether species, such as *N. pulchra*, which have been demonstrated to resist invasion in small experimental studies, are able to do so in an active agricultural landscape. It also will require intensive ongoing management, such as well-timed burning, grazing, or mowing (Hatch et al. 1999; Dyer 2003) to favor native grass species, or herbiciding to control aggressive non-native species (Anderson 1993; Stromberg and Kephart 1996; Corbin et al. 2004).

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URBAN RIPARIAN RESTORATION: AN OUTDOOR CLASSROOM FOR COLLEGE AND HIGH SCHOOL STUDENTS COLLABORATING IN CONSERVATION

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ABSTRACT

Despite the biological, social, and physical challenges that exist in urban creek restorations, there are opportunities to effectively involve local residents in ecological rehabilitation projects. An urban riparian restoration project along Strawberry Creek (Berkeley, CA) began with the goal of removing exotic vegetation and restoring native plant coverage. However, through the involvement of local high school and college students, the project accomplished an additional goal of educating the local community about restoration and conservation. Undergraduate students at the University of California, Berkeley conducted pre-restoration vegetation surveys of species richness and cover in order to assess initial species composition at the restoration site. Berkeley High School students, under the guidance of UC Berkeley graduate student mentors, removed exotic vegetation from an 800 m^2 area of the riparian zone and replaced exotics with over 500 individual native plants. Post-restoration vegetation surveys found that this project succeeded in reducing the cover of exotic vegetation and increasing native species richness. A smaller area adjacent to the student plantings was more intensively maintained by the University of California, Berkeley Office of Environment, Health & Safety and had a higher survival rate among the natives planted. Student attitudinal surveys indicated that students' involvement in the restoration activities increased their awareness and appreciation of the creek's value and educated them about scientific concepts of restoration and conservation. In spite of the various challenges of coordinating several interest groups, the involvement of local students has the potential to increase the likelihood that the project will succeed in the long term, especially if such involvement signals greater appreciation for the creek habitat.

Key Words: exotic vegetation removal, riparian, restoration, students, urban.

Urban creeks present tremendous challenges in efforts to reduce exotic riparian vegetation and maintain native biodiversity. Some of the challenges associated with restoring urban areas include: high frequency of disturbance, hydrologic alterations, exotic plants used in landscaping, bank erosion, increased levels of nutrients, and the presence of pollutants in runoff and litter (Walsh et al. 2005; Paul and Meyer 2001). Another challenge in urban restoration is the potential for negative public opinion towards the project, such as concerns about poor aesthetics, decreased safety, or a perception that the landscape appears to be too "wild" (Schroeder 1982; Gobster 1999; Bright et al. 2002). Such negative opinions can hamper the support for, and implementation of, a restoration project.

Despite the challenges involved in urban creek restorations, there are many opportunities to successfully achieve important conservation goals (Kondolf 1998). The high visibility and proximity of urban creeks to local residents can serve the vital purpose of encouraging conservation and restoration (Riley 1998). Furthermore, the involvement of local citizens, particularly students, can educate the local community about the benefits of riparian restoration and lead to improved attitudes towards restoration and conservation (Purcell et al. 2002). However, building local interest and involving amateur conservationists can be time-consuming, complicate the planning process, and affect the scope and intensity of a project (Morris and Moses 1999).

This study explores several elements involved in a riparian restoration project along Strawberry Creek in Berkeley, California. The objectives of this study were to: (1) compare pre- and post-

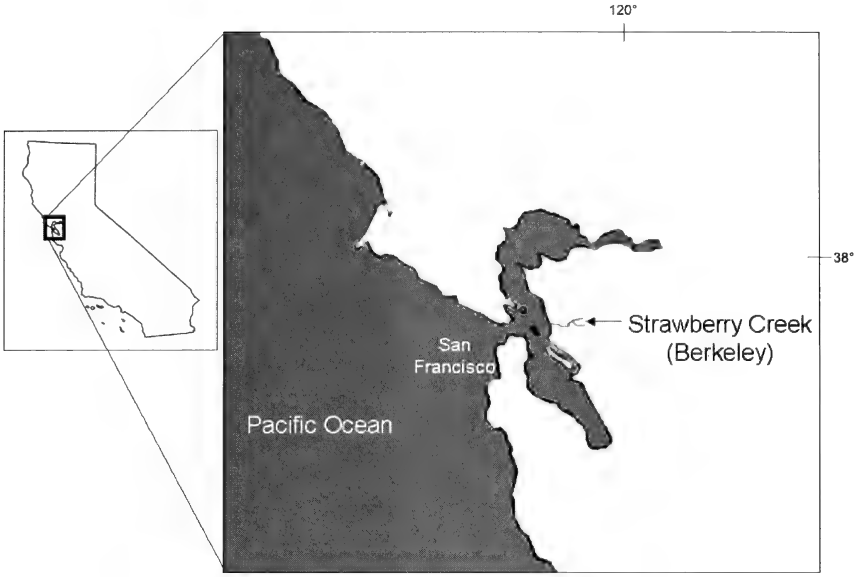

FIG. 1. Location map of the Strawberry Creek in Berkeley, California.

restoration vegetative cover (native versus exotic) at the restoration site, (2) evaluate the benefits and challenges of involving local students in the restoration project, and (3) examine the advantages and disadvantages of planning and implementing the restoration project through a collaboration involving several interest groups.

METHODS

Site Description. Strawberry Creek (37°52′N; 122°15′W) is located in Berkeley, California (Alameda County, USA) (Fig. 1). The Strawberry Creek watershed (4.7 km^2) is composed of two major branches: the north and south forks, which run in open channels through the University of California, Berkeley (UC Berkeley) campus (Charbonneau and Resh 1992) (Fig. 2). Downstream of the UC Berkeley campus, Strawberry Creek is primarily in underground culverts through the city of Berkeley until it discharges into the San Francisco Bay. While the upper Strawberry Creek watershed (Strawberry and Blackberry canyons) is composed largely of relatively undisturbed vegetation and intact riparian zones, the downstream watershed is urbanized with high levels of impervious surface including concrete and other channel alterations.

The restoration site is located at the very downstream end of the UC Berkeley campus just before Strawberry Creek runs into an underground culvert (Fig. 3). This area is known as the "Grinnell Natural Area" (named after the famous Berkeley naturalist Joseph Grinnell) and is relatively less developed compared to the rest of the campus. Despite its designation, the vegetation in this area is heavily dominated by exotic plant species including *Vinca major* (blue periwinkle), *Hedera helix* (English ivy), and *Eucalyptus globulus* (blue gum) (Nomenclature follows Hickman 1993.)

Previous restoration projects on Strawberry Creek include a management plan in 1987 that focused on improving water quality and reducing erosion and downcutting in the channel (Charbonneau 2000). Instream water quality was improved by eliminating direct discharges or cross-connections of the sanitary sewer system into the creek. Bank erosion and channel downcutting were addressed by implementing several erosion-control measures including the installation of a redwood cribwall and check-dams to reduce channel incision (Charbonneau and Resh 1992).

Project Description. The Strawberry Creek restoration (hereafter referred to as restoration project) was a native plant revegetation project in which the goals were to remove exotic vegetation in the riparian corridor, increase abundance and diversity of native species, and incorporate an educational component through the participation of local high school and college students.

Several steps were involved in the restoration project (an overview is presented in Table 1). A small planning committee met periodically to coordinate the organizational and logistical aspects of the project. Members of this committee represented several interest groups within UC Berkeley including staff, faculty, and students.

In March 2005, UC Berkeley graduate students involved in the Berkeley Natural History Museums' "Exploring California Biodiversity" project (funded by the National Science Foundation's GK-12 program) worked with an

FIG. 2. Aerial photograph of the upper Strawberry Creek watershed as it runs through the University of California, Berkeley campus (white line represents segments of creek that are above ground). The restoration site is located at the downstream end of the campus on the left bank of Strawberry Creek.

undergraduate plant ecology course at UC Berkeley to conduct initial weeding of the restoration site. The exotic plants removed consisted primarily of *H. helix* and *V. major*. Approximately 95 UC Berkeley students weeded an 800 m^2 area within the Strawberry Creek riparian zone and nearby upland areas within the Grinnell Natural Area. In addition to the initial weeding conducted in March 2005, weeding of exotics was done periodically throughout the project and on all the planting days.

In October 2005, approximately 80 high school students enrolled in an Environmental Science class at Berkeley High School transplanted native seedlings from flats into individual Conetainers® (Stewe and Sons, Corvallis, OR). The Conetainers, 2.5 cm diameter cylindrical cones, were in held in plastic flats (100 Containers per flat) for planting individual seedlings. The six native species planted (*Achillea millefolium*, *Bromus carinatus* (California brome), *Grindelia* sp., *Elymus glaucus* (blue wildrye), *Ranunculus californicus* (California buttercup), and *Aster chilensis*) were donated by a local non-profit organization (The Watershed Project). Once transplanted into the Conetainers, the seedlings were watered regularly until they developed sufficient root mass for planting into the ground.

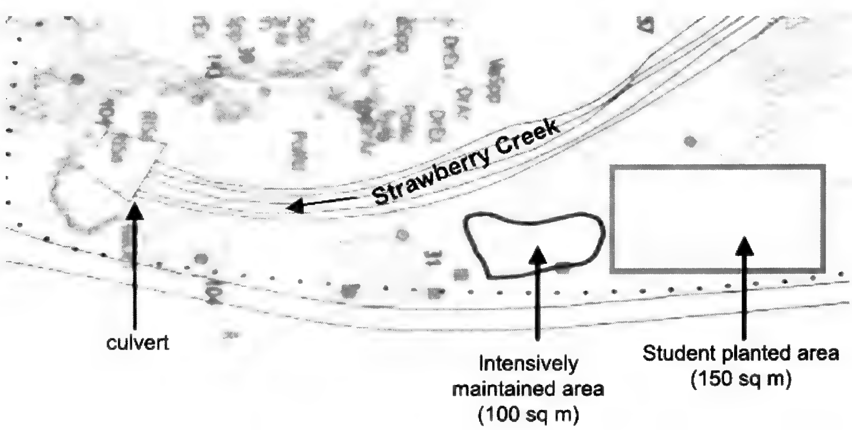

FIG. 3. The two areas of the Strawberry Creek restoration site within the Grinnell Natural Area: 1) an intensively maintained area and 2) a student planted area located on the left bank of Strawberry Creek just before it enters an underground culvert.

TABLE 1. TIMELINE OF TASKS COMPLETED AND GROUPS INVOLVED IN THE STRAWBERRY CREEK RESTORATION PROJECT DURING 2004–06. Abbreviations: BHS = Berkeley High School; EH&S = Office of Environment, Health & Safety; SCB = UC Berkeley chapter of Society for Conservation Biology; UCB = University of California, Berkeley; NSF = National Science Foundation.

Date	Task	Groups involved
2004–06	Periodic planning meetings to arrange logistical and organizational details	UCB faculty, staff (EH&S), graduate, and undergraduate students
2005		
March	Pre-restoration vegetation survey (established baseline conditions)	UCB Plant Ecology class (undergraduate students)
April	Initial weeding of site	UCB Plant Ecology class, BHS students, and NSF GK-12 graduate students
September	Acquired supplies (seeds, seedlings, soil, Conetainers etc.)	EH&S staff, UCB faculty, and graduate students
October	Fall weeding; transplanted seedlings from flats to Conetainers	Local non-profit organization (The Watershed Project), BHS students, and SCB members
Oct–Jan	Watered seedlings and allowed time for sufficient root mass to develop	EH&S staff and UCB graduate students
October	Collected cuttings for rooting, purchased plants from local nursery	EH&S staff and UCB graduate students
Oct/Nov	Installed informational signs and fencing at site	EH&S staff, UCB graduate students, and SCB chapter
2006		
January	Planted native seedlings into the ground	BHS students, EH&S staff, UCB graduate students, and SCB
Mar–June	Periodic spring weeding	EH&S staff, UCB graduate students, and SCB
May/June	Seed collection for fall planting	EH&S staff
June	Post-restoration vegetation survey	Authors (Purcell/Corbin)

In January 2006, approximately 100 high school students (from the same Environmental Science class at Berkeley High School that transplanted the seedlings in October 2005) planted the native seedlings from the Conetainers into the ground when soil moisture levels were adequate for seedling survival without watering. The seedlings were planted in a 150 m^2 "student planting area" (Fig. 3). In order to plant this area, the Berkeley High School students first weeded a circular plot (1-m diameter) and then planted several native seedlings species at evenly spaced intervals within the circular plot. The planted area was roped off to discourage human disturbance of the newly planted seedlings and informational signs were installed to explain the project to the public.

In contrast to the student planted area, a few staff members of UC Berkeley's Office of Environment, Health & Safety (EH&S) worked on an "intensively maintained area" (Fig. 3). Larger, more mature plants in 10 cm to 4 L pots were planted in this smaller area (100 m^2) and received more frequent maintenance (i.e., weeding, mulching, and watering). Approximately 300 individual plants consisting of 46 species were planted in the "intensively maintained area" (Table 2).

Vegetation Cover. In order to compare the vegetation cover before and after the restoration, species composition was sampled in the intensively maintained area in March 2005 (prior to removal of exotic species) and June 2006 (six months after replanting natives). At each sampling time, one 10 m transect was established perpendicular to the stream channel from the edge of stream. The transect included the riparian area near the stream bank and extended out to the edge of the restored area. Presence and percent cover of all plant species within a 0.25 m^2 quadrat was recorded every 0.5 m along the transect. Cover was estimated using cover classes (0–2, 2–5, 5–10, 10–25, 25–50, 50–75, and 75–100%). The numbers of exotic and native plant species in the 2005 (pre-restoration) and 2006 (post-restoration) were compared using ANOVA (SAS 2000).

Berkeley High School students in the Environmental Science class mapped the location and species of each seedling planted in January 2006 using graph paper to maintain a consistent scale. Landmarks such as fences and trees were documented to determine the proximity of the planting circles to specific features at the site. These maps were used to determine survival rates of the student planting area by comparing the initial maps with the surviving plants in June 2006.

Student and Leader Surveys. In order to gauge the educational and attitudinal impacts of involving students in the restoration project, a survey was given to 69 of the approximately 100 Berkeley High School students in the Environmental Science class who participated in restoration activities during 2005–06. The student

TABLE 2. NATIVE SPECIES PLANTED AT STRAWBERRY CREEK RESTORATION SITE.

Scientific Name	Common Name	Potted Plants	Conetainer Seedlings
Grasses, sedges, and rushes			
Agrostis pallens	Bent grass	7	
Bromus carinatus var. carinatus	Brome, California		100
Carex obnupta	Slough sedge	3	
Carex praegracilis	Deer-bed sedge	13	
Elymus glaucus ssp. *glaucus*	Blue wild rye	7	100
Elymus trachycaulus (RFS)	Slender wheatgrass	6	
Festuca californica	California fescue	1	
Hordeum brachyantherum	California meadow barley	4	
Juncus balticus	Baltic wire rush	4	
Juncus patens	Spreading rush	5	
Koeleria macrantha	June grass	1	
Melica californica	California melic grass	10	
Nassella lepida	Foothill needle grass	10	
Nassella pulchra	Purple needle grass	10	
Forbs and shrubs			
Achillea millefolium	Yarrow		100
Aristolochia californica	California pipevine	5	
Aster chilensis	California aster		100
Baccharis pilularis	Coyote bush	3	
Chlorogalum pomeridianum var. pomeridianum	Soap Plant	36	
Delphinium californicum	California delphinium	8	
Escholtzia californica	California poppy	1	
Fragaria vesca	Woodland strawberry	10	
Gnaphalium palustre	Western marsh cudweed	2	
Grindelia hirsutula var. hirsutula	Hairy gumplant	14	50
Helenium puberulum	Rosilla, Sneezeweed	16	
Heracleum lanatum	Cow parsnip	2	
Heuchera micrantha	Alumroot	10	
Iris douglasiana	Douglas iris	19	
Lonicera hispidula	Honeysuckle	20	
Lotus scoparius var. scoparius	Deerweed	2	
Lupinus sp.	Lupine	7	
Mimulus guttatus	Yellow monkey flower	2	
Physocarpus capitatus	Ninebark	2	
Prunella vulgaris	Common selfheal	4	
Ranunculus californica	California buttercup		50
Rhamnus californica ssp. *californica*	Coffeeberry	2	
Ribes menziesii	Canyon gooseberry	3	
Ribes sanguineum var. glutinosum	Red-flowered currant	3	
Prubus parviflorus	Thimbleberry	1	
Scrophularia californica ssp. *californica*	California Figwort, Beeplant	11	
Sisyrinchium bellum	Blue-eyed grass	1	
Stachys ajugoides var. rigida	Hedge Nettle	3	
Symphoricarpos albus	Snowberry, Bush	3	
Tellima grandiflora	Fringe cups	13	
Veronica americana	American brooklime	10	
TOTAL	46 species	294	500

survey consisted of six questions in which students were asked to evaluate what they learned and their resulting attitude towards the creek and restoration (Appendix I).

A survey was also given to a variety of individuals involved in planning, coordinating, and leading the Strawberry Creek restoration activities in order to evaluate their overall impression of the restoration. Questions focused on their involvement in the project, the motivation that kept them involved over time, challenges that arose, and whether the project had been a success (Appendix II). The leader survey also asked respondents to list the positive and negative aspects of the collaborative nature of the project.

RESULTS

Vegetation Cover. In March 2005, the plant community in the pre-restoration vegetation

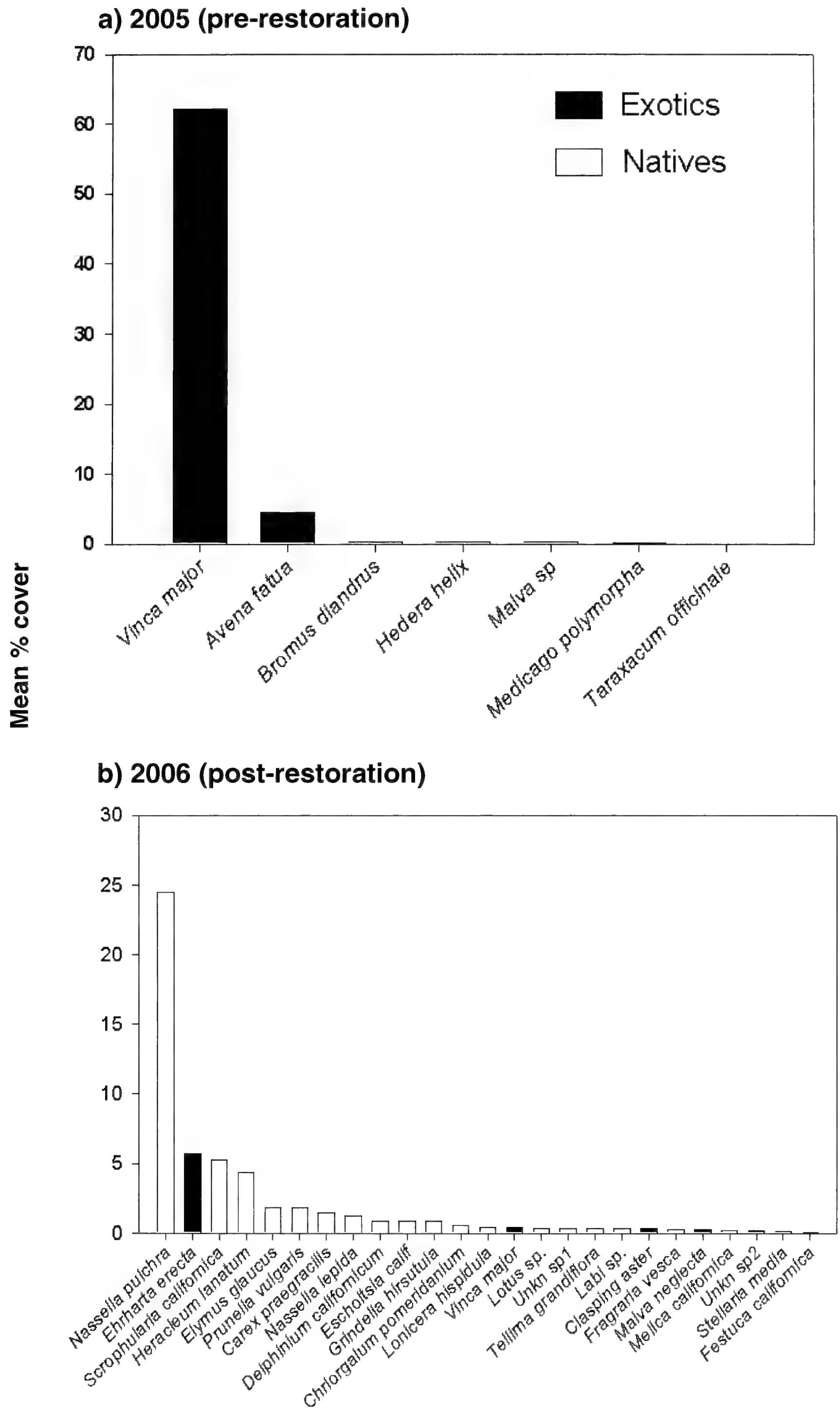

FIG. 4. Mean percent cover of species in 0.25 m^2 quadrats sampled along 10 m transects in: a) 2005 (pre-restoration) and b) 2006 (post-restoration). All species in Fig. 4a are exotics. Note the difference in scale between the two graphs.

survey was dominated by the exotic species *V. major* (mean cover = 62%) and no native species were recorded (Fig. 4a). *Vinca major* was the only species with a percent cover that exceeded 5% along the transect. Seven species were recorded along the entire transect; the average species richness in each quadrat was 2.0 (SE = 0.4) species 0.25 m^{-2}.

TABLE 3. SURVIVAL OF STUDENT PLANTINGS.

Scientific Name	Common Name	Survival rate
Achillea millefolium	Yarrow	71%
Grindelia sp.	Gum plant	35%
Elymus glaucus	Blue wild rye	28%
Aster chilensis	Aster	9%
Bromus carinatus	California brome	8%
Ranunculus californicus	California buttercup	0%
	Total Overall Survival:	30%

Following removal of *V. major* and subsequent planting of native species, species composition and prevalence of native species changed dramatically. In the post-restoration vegetation survey (June 2006), *V. major* was observed in only 5 of 20 points along the transect, and its cover was never greater than 2% (Fig. 4b). The richness of native species increased significantly post-restoration; 19 native species were recorded along the transect, with a mean native richness of 1.7 species 0.25 m^{-2} (SE = 0.3; significant difference in native species richness between pre- and post-restoration: $F_{1,28} = 13.2$, $p < 0.002$). Post-restoration mean native cover increased to 23.5% (SE = 6.1) per 0.25 m^2, while cover of exotics was reduced to 6.2% (SE = 4.3). The difference between pre- and post-restoration native cover was also statistically significant ($F_{1,38} = 2.0$, $p < 0.05$).

The survival of the student plantings was highly variable depending on the species (Table 3). For example, *A. millefolium* had a survival rate of 71%, yet none of the *R. californicus* survived. The overall survival rate of the student plantings was fairly low (30%) compared to the much higher survival rate of the "intensively maintained area" (~90%). Approximately 30 mature potted plants were planted in the "student planting area" and had a higher survival rate compared to the smaller Conetainer seedlings.

Student and Leader Surveys. The results of the student survey (n = 69) provided some insight on how much the students learned and their attitude toward stream restoration after their involvement in the restoration project. When asked: "What was the overall goal of the Strawberry Creek Restoration?" 91% of students were able to accurately state the goal of the restoration in their own words. When students were given a series of words to choose from that described their experience working on the restoration (i.e., fun, educational, boring, pointless) 49% of students responded that it was fun, 57% responded that it was educational, while only 32% responded that it was boring, and 12% responded that it was pointless. In addition, 55% of students remarked that working on the restoration project had a positive influence on their attitude towards the creek, such as an increase in awareness or appreciation of the creek. Lastly, when students were asked: "Do you think you'd be interested in working on stream restoration projects in the future?" 42% of respondents answered "yes" or "maybe."

When project leaders were asked about the advantages and disadvantages of the collaborative nature of this project, the common advantages listed were: (1) the educational aspect of involving students, (2) the committed leadership with a large breadth of expertise that shared responsibility, and (3) the cost effectiveness of using volunteers and donated materials. Some disadvantages mentioned were: (1) uneven enthusiasm from Berkeley High students, (2) quality control of plantings, and (3) difficulty of coordinating everyone's schedule. Overall, the positive aspects of the collaboration were mentioned more often than the negative aspects.

DISCUSSION

Restoration of Native Plant Biodiversity. The results of the pre- and post-restoration vegetation surveys indicated that the restoration project goals to remove exotics and replant natives were successfully achieved. The goal to remove exotic species was achieved through manual removal of the exotic plant species in the restoration area and was sustained over a one-year period (*V. major* cover decreased from 62% in 2005 to 1% in 2006). Mulching around the native plants also reduced the number of exotics that reemerged. The goal to replant the restoration area with native species was successfully achieved in both the student planting and the intensively maintained area with survival rate varying by plant species and level of maintenance.

The two restoration areas (student planted and the intensively maintained) varied in the effort to establish native species. The student plantings were completed at little to no cost (e.g., volunteer labor, donated supplies, no transportation costs—walking distance from high school campus) and covered a larger area (150 m^2). The low survival rate (30%) of the student plantings may be attributed to the small size of the seedlings planted and the low frequency of weeding and other maintenance over the spring season. Weeding and maintenance are known factors that influence the survival of plantings in restoration projects (e.g., Washitani 2001). During March and April of 2006, the small plants in the student planted area were rapidly outcompeted by exotic weeds such as *Malva neglecta* (common mallow), *Stellaria media* (common chickweed), *Hordeum murinum* (hare barley), *Avena fatua* (wild oat), *Medicago polymorpha* (California burclover), and *Ehrharta erecta* (panic

veldt grass). A few larger potted plants in the student planted area had a higher survival rate and were easier to locate during maintenance weeding. In contrast, the smaller intensively maintained area (100 m^2) was completed at a higher cost (~\$1500), but had higher survival rates among the native plantings (~90%). The reasons behind this success may be attributed to the larger size of the seedlings planted and higher frequency of weeding. A mulch path was also installed to prevent trampling of the native plants. Overall, a higher level of care and cost led to increased plant survival and a more aesthetically pleasing result.

The tradeoffs between cost, plant survivorship, aesthetics, and public involvement were important considerations in this project, as has been reported in other studies (e.g., Morris and Moses 1999). The competing goals of maximizing establishment of native species compared to keeping costs low required tradeoffs, but we believe that there were benefits of adopting both strategies within a single project. The intensively maintained area served as a "showcase" area with large native plants and low return of exotic plants. In contrast, the student planting area served an educational (and experimental) purpose while covering a larger area. Both purposes were of equal importance to this project.

Previous restoration projects have found that follow-up work is needed to ensure long-term success of a restoration project (e.g., Davies and Christie 2001). Higgs (1997) emphasized that in order for a restoration project to be successful it must exhibit durability (ability to persist for a long period). It has been suggested that a timescale of 15–20 yr is often a suitable timeline for evaluating the success of a restoration project (Mitsch and Wilson 1996). Therefore, despite the drastic decrease of exotic species abundance and cover at the restoration site during the first year, active management (such as weeding and mulching) will certainly be needed to prevent reinvasion of exotic species in the future (Berger 1993; Davies and Christie 2001; Washitani 2001). The urban location of the restoration site makes it more susceptible to reinvasion because of the large source of exotic propagules in surrounding areas. Active management of this project in the future will consist of manual weeding of exotics, additional planting of natives, and mulching around the native plants. EH&S staff are coordinating with Berkeley High School staff and student groups at UC Berkeley to carry out these efforts over the next few years.

During the winter of 2006–07, a second phase of restoration was completed with the primary goal of establishing native vegetation cover in the 2005–06 student planting area that had poor survival in the previous year. The methodology for 2006–07 plantings was equivalent to the previous year with a few modifications made based on the findings of the first phase of planting. The modifications included using larger four inch containers rather than Conetainers for September transplants by Berkeley High School students and intensive weeding in March and April 2007 by University staff and volunteers from a local creek restoration group (Friends of Five Creeks). The second phase of planting was accomplished with the assistance of approximately 100 Berkeley High School students in an Environmental Science class and 30 students from Kensington Hilltop Elementary School. As of June 2007, the results appear to be satisfactory with high plant survival in the student planting area.

Restoration as an Educational and Collaborative Exercise. The goal to incorporate an educational component in the restoration project was also successfully achieved through the involvement of local students from Berkeley High School. The students learned several scientific concepts from their involvement in the project including the importance of native biodiversity, differences between native and exotic species, and principles of ecology, plant physiology, and restoration science. An overview of these topics was introduced to the students at the beginning of each restoration activity to provide an educational context. Several of these topics were in agreement with the California State Board of Education Science Content Standards (California State Board of Education 2006). Students not only learned educational concepts, but also received hands-on experience in native plant restoration such as transplanting, weeding, planting, mulching, mapping, and determining where to plant each native species within the riparian zone.

While the initial purpose of involving students was purely educational, there were some other unexpected outcomes. In particular, it was compelling to see that 42% of students responded they were interested in working on restoration projects in the future. This suggests that involving students in restoration projects can serve not only an educational purpose, but can also inspire individuals to volunteer for other restoration projects in the future or perhaps even pursue careers in fields such as conservation biology, environmental science, or restoration ecology.

When considering the advantages and disadvantages of the collaborative nature of this restoration project, those involved in the leadership of the restoration project responded that strong and dynamic leadership was the key to a successful collaboration. The individuals involved in the planning and implementation of this project were motivated and committed to stay involved throughout the duration of the project and their breadth of experience resulted in a group dynamic where no single person was

solely responsible for getting the work done. Many of the leaders remarked that their passion for working with youth and environmental education kept them motivated, inspired, and involved in the project over the long-term.

Additional positive outcomes of the collaborative planning process were the connections formed between the many groups that worked on this project and the links to the community. The relationship established between the EH&S staff and the Berkeley High School teacher will ensure student involvement in the future. Interpretive signs describing the goals and progress of the project provided a link to the community to keep people informed of the changes occurring at the site. The student planting days were featured in the local news and the UC Berkeley campus website, furthering the connection between the University and the community. Ongoing updates and news about the restoration were made available online (University of California Berkeley 2006).

This project was also useful as a model of a restored ecosystem on the UC Berkeley campus and should serve to inspire future projects. The flowering and seed production of several planted native species in the spring of 2006 was an indication that the site may be able to sustain a new native plant community in the long term. However, weeding and maintenance over time will be crucial to keep the exotics from reinvading the site (Washitani 2001).

Recommendations. Upon reflection of the lessons gleaned from this project, we propose a series of recommendations for urban stream restoration projects. As mentioned previously, motivated and committed leadership was crucial for a successful collaboration and allowed the project to continue and flourish over time. Thus, we recommend that similar projects have at least one or two committed leaders who will oversee the other collaborators. Second, successful incorporation of students into restoration projects requires the enthusiastic participation of a classroom teacher who is willing to incorporate the restoration into their class' curriculum. Third, seed money and/or institutional support is required to acquire supplies (e.g., plants, potting soil, Conetainers) and maximize the efficiency of volunteer labor. Lastly, site location should take into account the proximity of the project to likely volunteers, to increase both numbers of volunteers and also participants' appreciation of the site. We hope that the lessons learned from this project can serve as a guide for similar restoration projects in urban areas.

Acknowledgments

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APPENDIX I.
STRAWBERRY CREEK RESTORATION STUDENT SURVEY QUESTIONS

1. What **activities** did you participate in as part of the Strawberry Creek Restoration on the UC Berkeley campus?
2. What was the **overall goal** of the Strawberry Creek Restoration?
3. Working on the Strawberry Creek Restoration was (circle all that apply):

fun educational boring hard work pointless

Other:

Has your attitude towards Strawberry Creek changed since your involvement in the restoration? (circle one)

Y / N

How has your attitude changed?

4. Do you think you'd be interested in working on stream restoration projects in the **future**?

Y / N

Why?

5. In general, what do you think are the **primary goals** of any creek restoration? (rank below)

__ Improvement of **water quality**
__ **Flood control**
__ Improvement of **Aesthetics / Beauty** of the neighborhood
__ Rejuvenation of **native biology/landscape**
__ **Recreational** uses
__ **Educational** tool for learning about nature/environment

Other:

APPENDIX II.
STRAWBERRY CREEK RESTORATION LEADER SURVEY QUESTIONS

1. How and when did you **first become involved** in the Strawberry Creek restoration project?
2. Please describe your **role/involvement** in the Strawberry Creek restoration project.
3. In your opinion, has this project been a **success** so far? (choose one)

Y / N

Why or why not?

4. What were some of the **challenges** faced in this project?
5. Looking back on how things have gone, what would you have **done differently** (if anything)?
6. What has kept you **motivated and involved** in this project over time?
7. Please list some of the **pros and cons of the COLLABORATIVE** nature of this restoration (i.e. involving Berkeley High School students, undergrads, grads, faculty, staff, non-profit organizations etc.).
8. What are your **visions/hopes for the future** of this project?

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LONG-TERM GROWTH AND PERSISTENCE OF BLUE OAK (*QUERCUS DOUGLASII*) SEEDLINGS IN A CALIFORNIA OAK SAVANNA

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ABSTRACT

We report on growth and survivorship of two cohorts of blue oaks *Quercus douglasii* Hook. & Arn. (Fagaceae) monitored at Hastings Reservation in Monterey County, California, the first growing in an unprotected old field and measured as seedlings in 1965 and the second planted as acorns in 1985 in several sites differing in their degree of protection from grazing. Growth of all individuals was extremely slow: among those surviving in the first cohort, mean ($\pm$ SD) height in 2006 was only 76.7 $\pm$ 45.0 cm for an average growth rate of 1.8 cm yr^{-1}, and only one of the original 73 oaks had grown taller than 1.5 m while one was still a seedling 28 cm in height 41 yr after being first marked. Of the second cohort, mean height 21 yr after planting was 54.3 $\pm$ 31.4 cm. None of these latter individuals had grown out of the sapling stage while 25% were still seedlings $<$ 30 cm in height. Growth of this second cohort was significantly greater when protected from grazing and when growing in the open rather than in the shade. Although growth was slow, survivorship of oaks first measured in 1965 was high, indicting that individuals can live for decades despite significant grazing pressure. Our results confirm the difficulties of inferring age from size of blue oaks, since individuals just achieving the height at which they are typically cored may be 50 or more years old. They also indicate that regeneration, although very slow, can occur in open oak savannas in California despite significant grazing pressure. Whether the observed amount of regeneration is sufficient for long-term sustainability will require continued monitoring and modeling of oak demography.

Key Words: blue oak, *Quercus douglasii*, regeneration, seedling growth, survivorship.

The health and status of California's vast oak woodlands is one of the more vexing questions currently facing the state's ecologists and rangeland managers. Are they declining, and if so, is it due to grazing, competition from exotic grasses, fire suppression, climate change, or some combination of factors (Griffin 1981; Muick and Bartolome 1987; Gordon and Rice 2000; Kueppers et al. 2005; Tyler et al. 2006)? In the case of the blue oak *Quercus douglasii* Hook. & Arn. (Fagaceae), a species dominating nearly 2 $\times$ 10^6 ha in the state (Standiford 2002), the evidence is mixed, as demographic surveys almost uniformly reveal limited recruitment but long-term studies have generally shown no decline in tree density (Tyler et al. 2006).

Resolving this problem lies in obtaining more extensive data on the demography of the species in question. Unfortunately this has not proved to be easy, since individuals can live hundreds of years and are logistically difficult to age, making it virtually impossible to estimate when prior regeneration events occurred, much less the extent to which such events are episodic and dependent on particular ecological circumstances.

Here we report on the persistence and growth of blue oaks planted as acorns or first marked as natural seedling recruits as part of studies going back to 1965. Our results indicate that the relationship between size and age in this species may be even more problematical than previously suspected. They also confirm the remarkable degree to which blue oak saplings can cling to what appears to be a precarious existence over many years until such time that they are able to achieve sufficient height to escape browsing.

METHODS

The study was conducted at Hastings Reservation, Monterey County, California, established in 1937. Thus, although cattle grazing, clearing, and various agricultural activities occurred historically, no such disturbances took place during the time period covered by this study. Hastings is located approximately 50 km from the coast and averages 53.3 cm of rain year^{-1} (mean of 67 yr between 1 July 1939–30 June 1940 and 1 July 2005–30 June 2006; records from Reserve headquarters). Individual oaks followed were either planted or monitored in two areas of the Reserve. The first, North Field, was an old field cleared around 1900 and used until 1937 for hay and grapes. North Field was left open the entire time

and was thus regularly grazed by mule deer (*Odocoileus hemionus*) as well as smaller mammals including gophers and mice. The second area (Arnold Road Flat) was within a large exclosure built in 1983 for a separate study and thus was not grazed by large herbivores during the study, but was open to smaller mammals.

Two sets of oaks were examined. The first, called the "White" cohort, consisted of 73 naturally-recruiting blue oak seedlings in North Field that were tagged and measured (height only) in April 1965 by K. L. White. Three of the seedlings were new in spring 1965. All others were pre-1965 seedlings when tagged. Their ages were not known, but all were short (mean $\pm$ SD = 6.5 $\pm$ 3.2 cm, range 2–18 cm) and were presumably thought to have been from acorns produced in fall of 1963 that sprouted in spring 1964. It was not possible to identify the original 1965 vs. pre-1965 seedlings, and thus all individuals in the White cohort are assumed to have been at least 42 yr old in 2006.

Subsequent to marking, seedlings and saplings were monitored and measured by J. R. Griffin on 10 occasions (June 1969, January 1976, September 1979, January 1984, June 1986, June 1987, August 1988, June 1989, June 1990, and February 1991). With some exceptions, at each sampling period the height of tallest sprout from each remaining seedling was measured, while starting in 1988, the greatest width of each seedling was measured. Finally, on 5 October 2006, we examined all individuals whose identity we could be confident of and measured their height, width, and the basal diameter of stems $>$ 0.5 cm at 5 cm above the ground. When multiple stems were present, they were combined to yield a single value for the overall diameter that matched the total basal area of all stems. Size and growth rates are based on the 14 individuals we identified and measured in 2006.

The second set of oaks used in the study, called the "Menke" cohort, consisted of individuals from a study of water relations of California oaks by J. W. Menke initiated in 1985. Blue oak acorns were planted in several 5 $\times$ 5 blocks varying in their degree of protection from grazing and openness. Block 1 (not protected; shaded) was planted adjacent to several blue oak trees near North Field, but otherwise not protected from grazing in any way. Block 2 (protected; open), also near North Field, consisted of acorns planted in the open, but protected by wire mesh baskets up to 40 cm in height that were opened up in 1992 to allow free growth of saplings that had in some cases had grown out of or up to the top of the baskets. Two additional sets of acorns were planted within a deer exclosure on Arnold Road Flat. Block 3 (protected; open) was planted in an open area within the plot, while block 4 (protected; shaded) was planted under partial cover of a mature blue oak within the plot; seedlings in both these blocks were also protected by wire mesh baskets 40 cm in height. For analysis, we divided individuals into those that were not protected (block 1) vs. protected (blocks 2–4)(variable "protection"), and those that were growing in the open (blocks 2 and 3) vs. those that were shaded (blocks 1 and 4)(variable "shade").

We measured the maximum height, maximum width, and basal diameter at 5 cm above ground on 5 October 2006 of all individuals we could unambiguously identify as having been from the original set of acorns based on remaining wooden stakes and their location within the original grid on which acorns were originally planted (Fig. 1). All individuals were thus known to be 21 yr old at the time they were measured. No data from prior years was available. We used the two categories of "protection" and "shade" to quantify the effects of these variables on growth of the saplings using general linear models. Survivorship could not be measured in these oaks, as we could not be certain how many had been planted initially.

Following Phillips et al. (1997), we classify individuals as "seedlings" ($<$30 cm in height), "saplings" (30–150 cm in height), "poles" (150–300 cm in height), and "adults" (taller than 3 m). Significant browsing by deer, where present, is expected up until individuals reach the pole size class (McCreary 2001). Values presented are means $\pm$ SD.

Results

White Cohort

Of the original 73 seedlings marked in 1965, J. R. Griffin found 64 (88%) in June 1969 and 18 (24.7%) in February 1991, while we successfully located 14 (19.2%) in 2006 (Fig. 2). These values represent minimum survivorship of the original seedlings, since other seedlings and saplings were present in the plot and it is possible that some lost their tags during the course of the study and could no longer be identified.

Growth of the seedlings varied considerably, with individuals at the end of the study an average of 76.7 $\pm$ 45.0 cm (range 28 to 200 cm) in height (Fig. 3), 90.6 $\pm$ 43.8 cm (range 13 to 174 cm) in width, and 4.3 $\pm$ 2.0 cm (range 0.7 to 7.7 cm) in basal diameter. The rate of growth was $<$ 1 cm yr^{-1} in height during the first three decades (Fig. 4), and in one case (7% of surviving individuals) the oak was still in the seedling category (28 cm in height) in 2006, 41 yr after being initially marked. Of the remaining 13 oaks, 12 (86%) graduated to the sapling size class by 2006 and one (7%) achieved pole status, thereby being the only one of the original 73 seedlings to

FIG. 1. One of the Menke plots in December 2006. The wire mesh exclosures are approximately 40 cm in height. Note the wooden stakes and grid spacing of the seedlings used to identify them in 2006.

have completely escaped likely grazing by deer after (at least) 42 yr. Overall, the mean increase in height over the 42 yr was 1.83 cm yr^{-1} (range 0.67–4.76 cm yr^{-1}) and the mean increase in basal diameter of the 14 oaks (conservatively assuming that their original diameter was 0) was 0.10 cm yr^{-1} (range 0.05–0.18 cm yr^{-1}).

Although overall growth was slow, growth rate increased considerably near the end of the study (Fig. 4), presumably as height or width finally became sufficiently large to provide some protection against grazing. Overall, height was relatively well predicted by models including age as either a squared or exponential term (quadratic model: height = $-0.866 * \text{age} + 0.054 * \text{age}^2 + 15.1$, $F_{2,160} = 81.7$, $R^2 = 0.50$, $P < 0.0001$; exponential model: height = $9.27 * e^{0.0399*\text{age}}$, $F_{1,161} = 140.8$, $R^2 = 0.46$, $P < 0.0001$).

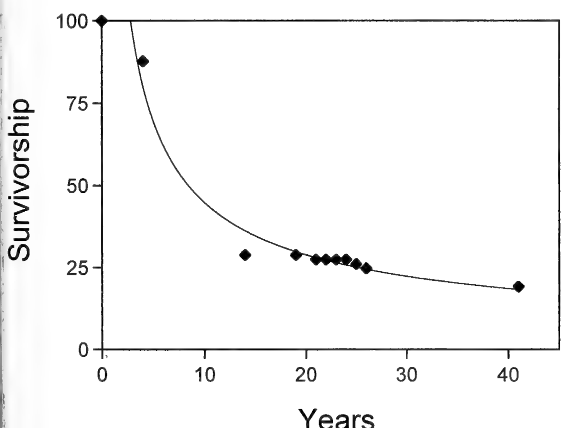

FIG. 2. Survivorship curve for the 73 White cohort first marked in 1965 as seedlings. The overall annual survivorship between 1965 and 2006 based on this sample is 96.1% $year^{-1}$. Line drawn is fit by a power curve: percent survivorship = $193.3 \times (\text{years})^{-0.634}$.

Menke Cohort

We identified and measured a total of 32 oaks in the four Menke plots (Fig. 4). Overall, the mean height of the individuals in 2006 was 54.3 ± 31.4 cm (range 6–112 cm), while the mean diameter was 1.6 ± 0.5 cm (range 0.6–2.8) cm. After 21 yr, 8 of 32 (25%) were still seedlings < 30 cm in height, while the majority were saplings < 150 cm in height. Mean increase in height was 2.59 cm yr^{-1} (range 0.29–5.33 cm yr^{-1}) and mean increase in diameter was 0.074 cm yr^{-1} (range 0.029–0.133 cm yr^{-1}). Both protection (positively) and shade (negatively) affected height of the oaks, while only shade (negatively) influenced diameter (Table 1). At 21 yr of age, the height of these individuals was generally within the range expected from the White cohort, given that none of the latter had been protected from grazing in any way (Fig. 4).

DISCUSSION

Because of low survivorship, there have been few prior studies of growth by blue oaks seedlings and none that have covered as long a time period as that reported on here. Previous work by Phillips et al. (1997, 2007a, b) is the most extensive, demonstrating that up to 18% of blue

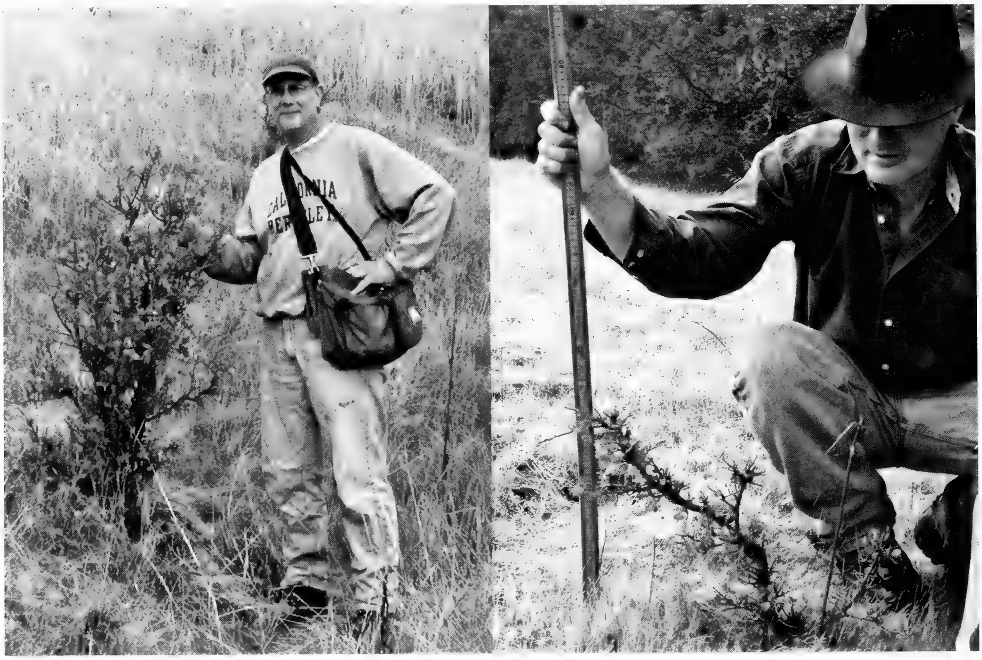

FIG. 3. The authors at two of the White individuals in October 2006. Left: tree 767, 7 cm in height in 1965, 112 cm (6.7 cm diam.) in 2006, by which time it was third-tallest tree of the 14 found. Right: tree 772, also 7 cm in height in 1965, 34 cm (1.9 cm diam.) in 2006, at which time it was the second-shortest tree still extant.

oak seedlings are 26 or more years old, that surviving seedlings grow very slowly and remain for a long time in the seedling size class, and that fencing significantly increases seedling growth. Our results confirm and extend these conclusions. Of 14 oaks known to have survived 41 yr after being marked, one (7%) was still a seedling 28 cm in height and only one successfully outgrew the sapling stage (>150 cm) during the course of the study.

Comparably slow growth was observed in a second set of oaks planted as acorns in 1985, one-fourth of which were still seedlings < 30 cm in height when 21 yr old. Growth in this second set was significantly greater among those that were protected from grazing by wire mesh baskets and (in some cases) deer fencing and among acorns that were planted in the open rather than in the shade. The latter of these findings matches the reduced photosynthetic capacity and root elongation rates among blue oak seedlings grown in the shade by Callaway (1992a, b), although Callaway's studies also found blue oak seedlings to be relatively shade tolerant and to survive better when cover was present.

In contrast, the first of these findings, that growth of seedlings was greater among those protected from grazing, is not surprising, as grazing by deer and rodents is well known to inhibit seedling growth (White 1966; Griffin 1981; Muick and Bartolome 1987; Tyler et al. 2002; Phillips et al. 2007a). However, growth rates were still low, even among individuals protected from grazing by large herbivores and, at least to some extent, by rodents as well. Of nine oaks growing within deer exclosures and protected by 40 cm wire mesh baskets, mean height after 21 yr was still only 65.6 cm (range 32–112 cm) and mean increase in height only 3.12 cm yr^{-1} (range 1.48–5.33 cm yr^{-1}).

Thus, under natural conditions, blue oaks at Hastings Reservation grow very slowly and may require several decades or more to outgrow the sapling stage even when protected from most sources of grazing pressure. Only after decades, once both the above-ground size of saplings is sufficient to provide some protection against uninhibited grazing by deer and other large herbivores and (perhaps in some cases) the below-ground roots are deep enough to access a more reliable water source, does the growth rate increase (Fig. 4).

Although growth was slow, even among protected seedlings, survivorship of seedlings was relatively high even when unprotected. Of 73 unprotected seedlings originally marked in 1965, 64 (88%) were alive four years later (Griffin 1981), for an annual survivorship of 96.8%, far higher than reported in other studies (Davis et al. 1991; Allen-Diaz and Bartolome 1992; Phillips et al. 2007b). Survivorship subsequently declined, but at least 18 (24.7%) were still alive 26 yr after marking in 1991 and 14 (19.2%) were alive in

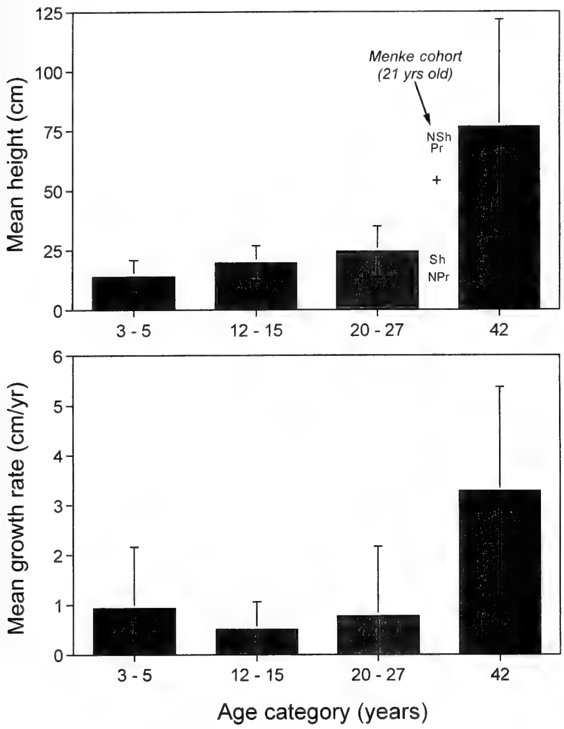

FIG. 4. Mean ± SD height (top) and mean ± SD annual increase in height (bottom) of the White cohort during the four decades of the study. Also marked in the top panel in between the last two categories are the mean heights of the 21-year-old Menke cohort, including the overall mean (+) and the means for seedlings that were not shaded (NSh), protected from grazing (Pr), shaded (Sh), and not protected from grazing (NPr).

2006, 41 yr after the start of the study. Thus, the overall survivorship of the 73 seedlings over the course of the study was at least 96.1% year^{-1}, and survivorship during the 15 yr between 1991 and 2006 was an impressive 98.3% year^{-1}. Possibly these high values are in part a result of having followed a cohort of seedlings that had already undergone considerable mortality by the time they were marked in 1965. Nonetheless, the ability of the seedlings to persist despite repeated and apparently intense browsing over decades is impressive.

Previous studies have found significant differences between the actual age structure of blue oaks stands based on tree-rings and the predicted age structure based on diameter (McClaran and Bartolome 1990; Phillips et al. 1997). Our results suggest that in at least some cases there may be even greater discord between age and size of blue oaks than previously thought because of the length of time some individuals require to achieve the height necessary to escape significant browsing damage. Of the oaks in the White cohort, only one (1.4% of the original sample) had achieved a height of over 150 cm in 41 yr, making it into the "pole" stage at which browsing by large herbivores was no longer likely to significantly inhibit further growth. Conversely, one individual remained a seedling 28 cm in height 41 yr after being first marked. In the Menke cohort, only a small proportion of individuals (3 of 32, 9.4%) had achieved 1 m in height by age 21, and none had successfully grown out of the sapling stage. Clearly by the time many of these oaks graduate into the adult population they will be well over half a century old, and in some cases possibly much older, assuming they survive. At that point, measuring their diameter at breast height (DBH) will clearly yield a gross underestimate of their age. More problematically, even coring them will not provide a good estimate of their actual age, since individuals may have been 50 or more years old by the time they reach the height at which coring is generally performed.

A recent review of recruitment in blue oaks concludes that resolving the current controversy over the sustainability of California oak woodlands will require long-term monitoring, age-structure analysis, and population modeling (Tyler et al. 2006). Our results add to previous concerns that the second of these, age-structure analysis, will have to be conducted with caution and that even with extensive coring or clearing (Mensing 1992) it may not be possible to accurately pinpoint the years or even the general time periods when regeneration has taken place in the past in established stands.

With respect to the regeneration of blue oaks, our sample is clearly too small to draw many

TABLE 1. RESULTS OF TWO-WAY ANOVAS ANALYZING THE VARIABLES "PROTECTION FROM GRAZING" (PROTECTED, NOT PROTECTED) AND "SHADE" (SHADED, NOT SHADED) ON HEIGHT AND DIAMETER OF THE MENKE COHORT IN 2006, WHEN THEY WERE 21 YRS OLD.

	Mean ± SD (N)			
	Yes	No	*F*-value	*P*-value
Height (cm)				
Protection	68.4 ± 23.1 (24)	13.0 ± 4.8 (8)	4.49	0.043
Shade	20.1 ± 13.1 (11)	72.2 ± 21.6 (21)	8.80	0.006
Diameter (cm)				
Protection	1.67 ± 0.57 (24)	1.26 ± 0.39 (8)	2.67	0.11
Shade	1.13 ± 0.40 (11)	1.80 ± 0.49 (21)	13.8	0.001

conclusions. However, it is noteworthy that survivorship of naturally recruiting seedlings was relatively high, at least subsequent to when they were first marked. Furthermore, although only one of the original 73 seedlings had successfully grown out of the sapling stage after 41 yr, other individuals in this sample may eventually join it. Thus, regeneration is occurring, albeit at a painstakingly slow rate. Whether such a slow rate of regeneration is sufficient to maintain California's blue oak woodlands over the long term remains to be determined.

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PATTERNS OF CARBONATE DUST DEPOSITION: IMPLICATIONS FOR FOUR FEDERALLY ENDANGERED PLANT SPECIES

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ABSTRACT

The calcareous soils in the San Bernardino National Forest host a group of endemic plant species, including five listed as federally endangered. The parent material for these soils is a very pure deposit of magnesium and calcium carbonate that is being actively mined. The mining operations produce copious quantities of dust. This study evaluated the quantity of dust moving across the landscape and depositing to the ecosystems, and the effect of carbonate dust on physiological parameters of a plant species acting as a surrogate for the endangered species. Most of the dust was found to deposit within one kilometer of the mining operations. Plants growing within the deposition zone had lower photosynthetic activity and less vigorous growth patterns. Several mitigation measures are recommended.

Key Words: calcareous soils, carbonate dust, dust deposition, passive monitoring.

Dust is the most common air quality problem in arid and semi-arid ecosystems. The effects of anthropogenic dust on native vegetation do not receive as much research attention as does the effects of gaseous pollutants. In part, it is because "dust" is a site-specific parameter dependent on the events or mechanisms of generation and the geologic source (Reheis et al.1995). The effects of dust deposition on plant biology and ecological function are also site specific (Farmer 1992). Both of these effects are dependent on weather and climate conditions, and characteristics of the plant community. Furthermore, damage caused by dust can vary from physical effects such as abrasion and surface coating, to chemical effects such as alkalinity due to limestone deposition or heavy metal toxicity due to road and fly ash deposition. Unlike gaseous air pollutants, which usually cause one or two symptoms related to the chemical behavior of the gas, deposition of particulate dust causes multiple responses controlled by a wide array of variables, such as wind speed, chemical composition, and particulate size.

The four common sources of dust are urban secondary aerosols, road dust (both from paved and unpaved surfaced), dust created by cement manufacturing, and open pit or strip mining – particularly limestone mining (Bačić et al. 1999; Ashbaugh et al. 2003). In this study, we evaluated the distribution of particulates and the effects of limestone mining and crushing activities on an endemic calcareous plant community in the San Bernardino Mountains of Southern California.

The Sentinel Crusher site is on the San Bernardino National Forest and leased to the OMYA Inc., an international company with North American headquarters in Proctor VT. It is located in Holcomb Valley on the north slope of the San Bernardino Mountains in southern California. OMYA Inc. actively mines dolomite deposits from open strip mines. Dolomite is a sedimentary rock containing both calcium carbonate and magnesium carbonate (collectively referred to as "carbonates"). It is a common treatment for neutralizing acid soils in agricultural systems, and as is the case for dolomite mined at the Sentinel site, it is commonly used in medical products and medicines. Dolomite mining activities such as blasting, excavating, processing, and vehicle movement to transport rock and tailings, produce large amounts of fugitive dust (Farmer 1992).

Calcareous soils developed from limestone or dolomitic parent materials provide unique habi-

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tat for many endemic plant species globally (Krunkeberg 2002). Ten rare plants in the San Bernardino Mountains occur only in localized pockets of carbonate substrates (USFWS 1997). Of those species, *Acanthoscyphus parishii* (Parry) Small var. *goodmaniana* (Ertter) Reveal (i.e., *Oxytheca parishii* Parry var. *goodmaniana* Ertter; Cushenbury oxytheca; Polygonaceae) and *Eriogonum ovalifolium* Nutt. var. *vineum* (Small) A. Nelson (Cushenbury buckwheat; Polygonaceae) are federally endangered with populations in the Holcomb Valley. Protection of these species is addressed in a U.S. Fish and Wildlife Service recovery plan (USFWS 1997b), and habitats of both are threatened by future expansion plans at the Sentinel Crusher site.

Our first objective was to measure and describe the distribution and deposition of carbonate dust in the complex terrain around the mining operation. The distribution of carbonate dust depends greatly on wind speed, wind direction, and particle size, with smaller particulates (<20 μm) able to enter long-term suspension and travel great distances. In addition, as with most limestone mines, the site managed by OMYA Corporation, is located in mountainous terrain making *a priori* estimates of direction and concentration of limestone dust generated by the mining activities difficult. The interactions of precipitation, temperature, geologic substrate, and wind speed on aerlization and subsequent deposition of dust are complicated (Reheis et al.1995; Reheis and Kihl 1995). Because it was critical to understand detailed deposition patterns, we developed a passive sampler that enabled us to monitor deposition of $Mg/CaCO_3$ at 30 locations along seven transects radiating in ordinal directions from a central point at the limestone crusher. We also deployed two real time electronic particulate monitors to provide information on atmospheric loads adjacent to the crusher and 600 m away.

Our second objective was to assess the effects of deposition on plant productivity. Because experimental manipulation of protected plant species is prohibited, we selected a surrogate species, *Eriogonum microthecum* Nutt. var. *corymbosoides* Reveal (Polygonaceae) to measure physiological characteristics and phenology.

The most obvious effect of dust deposition on plant biology is surface coating, which reduces light availability and therefore CO_2 assimilation. Gale and Easton (1979) investigated loading of leaf surfaces due to limestone mining in Israel and found that leaves reached a maximum surface loading of 15.2 mg cm^{-2} (152 g m^{-2}) and that the gradient in deposition declined to near background concentrations (1.4 mg cm^{-2} [14 g m^{-2}]) at 1.1 km. In their study, they detected little deleterious effects of dust. Several other studies have, however, shown significant reduction in CO_2 assimilation with increased dust accumulations (Farmer 1992). Some studies have suggested that since many dust particles are an ideal size to lodge in open stomata, perhaps reduction in water use efficiency and increased drought susceptibly may result from dusty environments (Eveling 1986; Manning 1971). Subsequent studies have shown both increases and decreases in transpiration (Farmer 1992) suggesting that the physiological parameters of photosynthesis, respiration, and transpiration are so closely linked that establishment of a single response is impossible.

Since the greater concern is usually productivity of agricultural or native vegetation, phenological methods have been used to establish direct links between dust deposition and productivity. In the arid Mojave, road dust caused early senescence of leaves and reduced photosynthesis (Sharifi et al. 1997). In the Appalachian Mountains, a mesic mixed hardwood forest impacted by limestone mining had smaller leaf areas in deciduous tree species and reduced apical growth in hemlocks (Brandt and Rhoades 1972). The Appalachian study also suggested that the ultimate ecological response was a shift in species composition. This, of course, is a major concern of land managers for endemic species and in developing habitat protection plans for threatened and endangered plant species in unique habitat.

This report describes the atmospheric dispersion pattern of limestone dust, provides details of a passive deposition monitoring method, and examines the effects of dolomitic limestone deposition on plant physiology and phenology.

Materials and Methods

Study site. The Sentinel mine and crusher are located on the northeast side of the San Bernardino Mountains in the rain shadow of coastal storms (Fig. 1). The vegetation is characteristic of the San Bernardino Mountains in the Transverse Ranges subregion of the Southwestern California region of the California Floristic Province, but also carries some elements of the Desert Mountains subregion of the Mojave Desert region of the Desert Province (Hickman 1993). The area is home to a community of endemic calcareous plant species.

Most of the open strip mines and the rock crushing operation are on an east-facing slope. The terrain is rugged and steep to the north, and although flatter to the south, the landscape contains patches of dense standing vegetation, and dense patches of down and dead trees and shrubs. Mining has been active in the area for many years so there are many remnants of past activities scattered throughout the area including open pits, slag piles, and tailings.

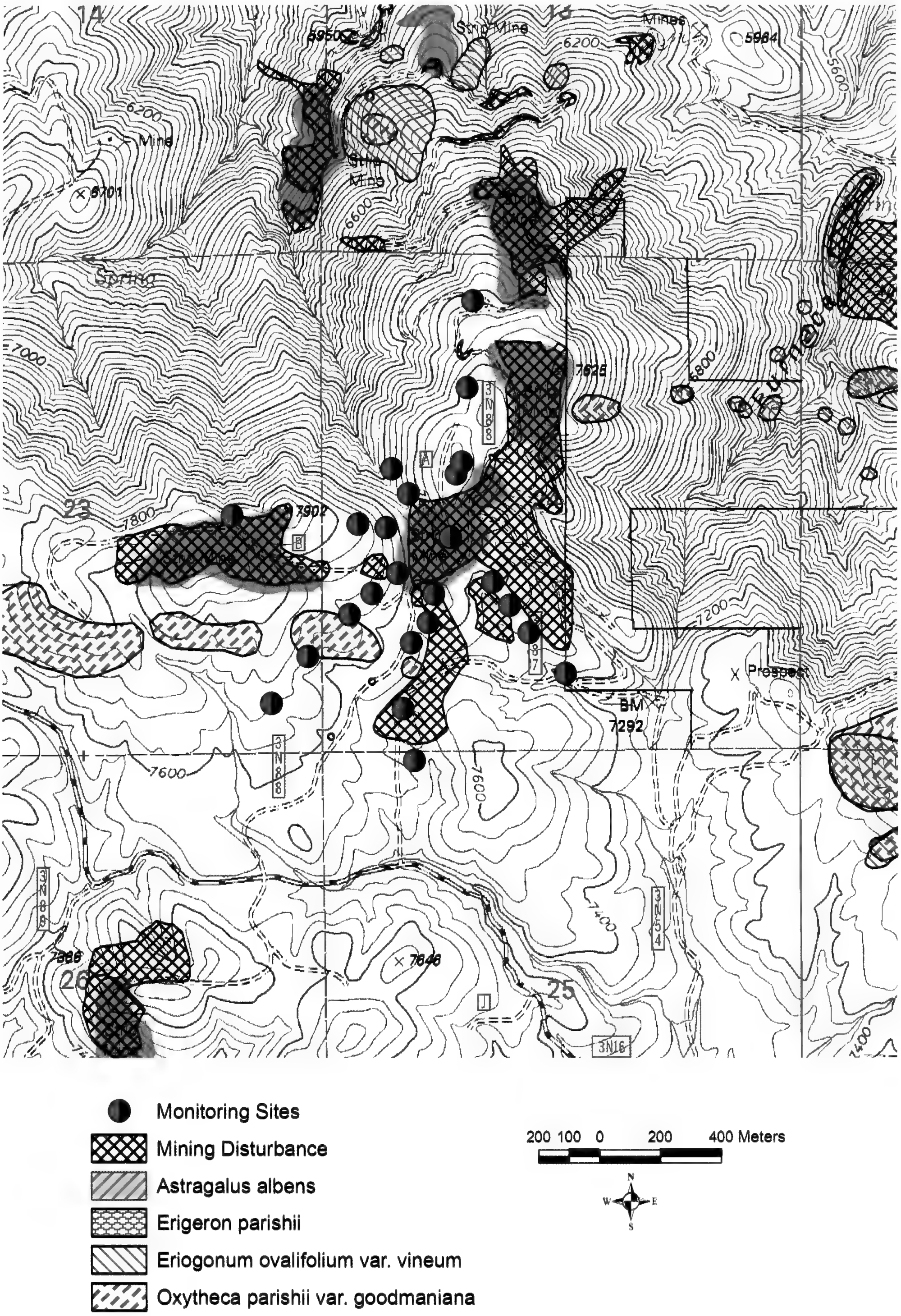


FIG. 1. Local topography and location of mining activities, plant populations and sampling sites. This map was produced with cooperation of the San Bernardino National Forest.

Preliminary survey. Deposition patterns on foliage, estimates of dust size, and evaluation of dust particles lodging in stomata was conducted in a preliminary survey. Leaf samples were collected from individuals adjacent to mining activities and at 1 km away from activities. Leaf specimens were examined with an XL30-FEG SEM (Philips, New York, NY) that uses a field

emission electron gun with a Schottky emission cathode. Samples were affixed to aluminum mounts with double stick carbon tape (Ted Pella, Inc., Redding, CA) and sputter coated with gold and palladium using an Emscope Sputter Coater 500A (Quorum Technologies, East Sussex, UK). Samples were placed approximately 40 mm from the target material (cathode) and coated at a deposition rate of 15–18 mA for 105 sec. Images were captured digitally.

Study design. This study was conducted during the late summer and fall of 2003 and from spring (April) through fall of 2004. Dust distribution data are from the full growing season of 2004, as are the plant productivity data. Meteorological data and data from the DataRam particulate monitors from the fall 2003 season, as is the photosynthesis information.

The study was conducted in a 1 km radius area around the crusher. Passive monitoring sites were established along transects in ordinal directions from a center point creating concentric circles around the center point (34°19′47.85″N, 116°56′21.35″W). The center point was as close to the main point source of dust, a rock crusher, as we could safely locate it (Fig. 1). Individual sampling sites along each transect were located 200, 300, 400, 600, 800, and 1000 m from center in the ordinal directions of N, NW, W, SW, S, and SE. Sites are described throughout this paper by direction and distance from center (e.g., N200 is located 200 m north of the center point). A few monitoring sites deviated from their planned location or were eliminated because of roads, obstructions, or impassible terrain. No sites were set up to the northeast due to inaccessibility and steep terrain and only a single site at 1000 m was established east of the crusher.

Portable weather stations (Onset Computer Corp, Pocasset, MA) were set up at N200 and SW600. Wind speed and direction, temperature, and relative humidity were recorded every 10 min by a HOBO weather station data logger. The data loggers were downloaded using BoxCar® Pro 4.3 at 3- to 4- week intervals. At both weather stations, Portable Particle Sizing Aerosol Monitor/Data loggers (model DR-4000, TermoAnderson, Smyrna, GA) were installed. The DR-4000s are continuous, real-time monitors, which determine particle size (μm) and mass concentration levels (μg m^{-3}), reporting the data to internal dataloggers at user-determined intervals. The sampling flow rate was 1.0 L min^{-1}, readings were automatically averaged every 10 sec with a resolution of 0.0001 mg m^{-3}; and means of the averages were then recorded every 10 min. The DR-4000 aerosol monitors were gravimetrically calibrated to dolomite particles collected from the crusher site, following the ThermoAnderson® protocol, prior to placement in the field.

The passive collectors were constructed from plastic jars, 55 mm deep with a 65 mm diam. opening. To keep deposited particles trapped in the jars, each cup contained a 20 mm thick loosely-spun fiberglass filter. The passive collectors were fastened to a rebar stake at 1.0 m above the ground at each sampling site. Passive collectors were transported to and from field sites sealed and exchanged every 3–4 wks from August 25, 2003 to October 22, 2003, and from April 2004 to October 2004. Both unopened field blanks and lab blanks were used to evaluate background and potential contamination from transport.

The amount of carbonate deposited in each cup was determined by chemical analysis (Goh et al. 1993). Twenty mL of 0.4 M acetic acid was added to each collector. The jars were sealed, shaken for 30 sec, and allowed to react for 30 min, after which the pH of the solution was measured. The analysis was based on the neutralization reaction of 0.4 M acetic acid with $Mg/CaCO_3$. Milligrams of $CaCO_3$ in each collector were calculated from a standard curve with a range of 2 to 500 mg $CaCO_3$.

In addition to passive collectors, direct deposition to plant leaves was measured at 11 of the passive sites where the appropriate surrogate species was present. Five leafy stems of one individual per site were washed on August 25, 2003 with 5% acetic acid and then rinsed with nanopure water. The method was developed in a series of controlled laboratory experiments prior to use in the field. Tests were conducted using stereoscopes to determine the optimum washing method with a minimum of physical damage to the plants. One leafy stem from each plant was collected every 3–4 wk when passive cups were exchanged, making readings cumulative. Chemical analysis for $CaCO_3$ was performed in the same manner as for the passive collectors above. The leaf area for each sample was measured using a LI-3100 leaf meter (LiCor Inc., Lincoln NE) and deposition of carbonate dust on the photosynthetic tissue (both stems and leaves) was recorded as mg cm^{-2}.

A LI-COR® LI-6200 portable photosynthesis system was used to determine net photosynthesis (A), stomatal conductance (g_s), and transpiration (E) under ambient conditions. One small, leafy stem was sealed in a 250 ml leaf chamber for gas measurements and a flow rate of 200 μmol sec^{-1} was established. Ten plants were measured at each active monitoring site (N200 and SW600) on October 22 and 23, 2003 between 09:30 and 11:30, when photosynthetic rates for this species were maximal. Leaf area was measured using a LI-3100 leaf meter and entered into the LI-COR® LI-6200 prior to computing gas measurements. Photosynthetic measurements were repeated in 2004.

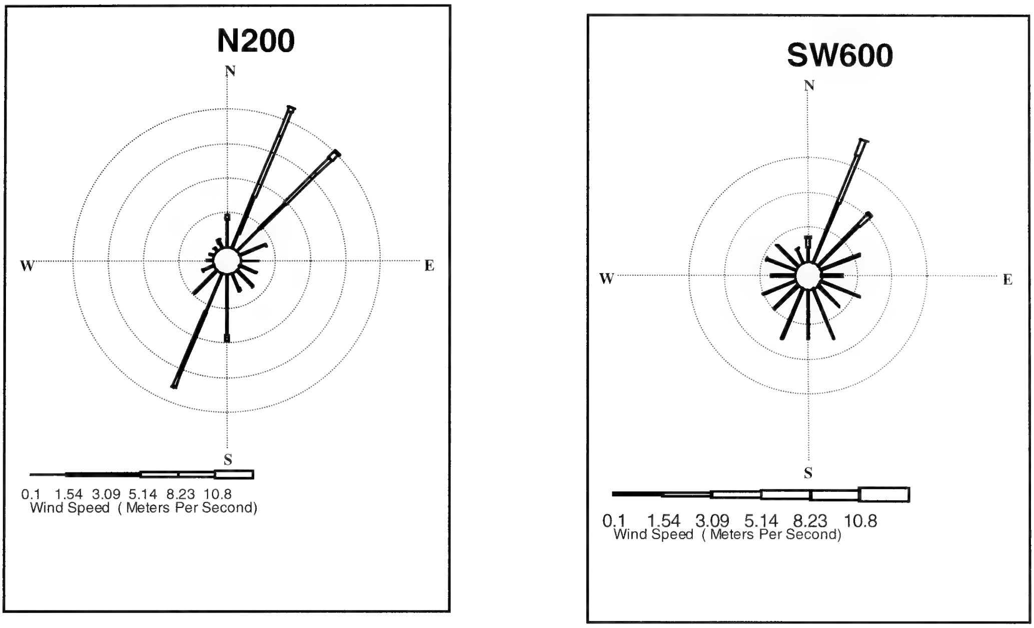


FIG. 2. Wind roses for August through October, 2003 at the N200 location adjacent to mining activities, and at SW600, partially shielded by juniper forest vegetation. Wind speeds and wind directions are the sums of 3 month exposures.

Phenological characteristics were measured three times during the growing season, in April, June, and September 2004. Ten plants at each of 3 locations (N200, SW600, and SE1000) were selected, and five shoots on each plant were marked for repeated measurements. The following parameters were determined: number of stems per plant, total shoot length, foliated shoot length, length of new growth on shoot, number of new branches on shoot, and number of flowers per stem.

Data analysis. The weather and aerosol data including wind speed ($m\ s^{-1}$), particle size (μm), and mass concentration levels ($\mu g\ m^{-3}$) were analyzed using a Mann-Whitney Rank Sum Test for non-parametric data and treatments were considered significantly different when $P < 0.05$.

The passive cup sampling data passed both normality and equal variance tests once transformed to the negative log of the original dataset. The transformed data were then analyzed using a two-way ANOVA and reported as mean $\pm$ 1 standard error (SE) of the original data set. A (all-pairwise) multiple comparison test (Holm-Sidak method) was then used to determine significant difference (i.e., $P < 0.05$) among sites based on direction and distance, respectively. The data were analyzed and represented using the sum of three consecutive sampling periods between April and October 22, 2004.

Statistical analysis was not performed on the plant washing data due to lack of replication. However, the data are presented for each sampling period and site.

The gas exchange data met requirements for both normality and equality of variances once transformed to square (photosynthesis) and square roots (conductance and transpiration) of the original dataset. The transformed data were then analyzed using two-way ANOVA and were presented as mean $\pm$ 1 SE in untransformed units. Data were analyzed using Sigma Stat version 3.0 (SPSS Inc, Chicago, IL).

RESULTS

Wind speed was significantly different ($P < 0.001$) between the two active stations (N200 and SW600) with the N200 site (nearest the crusher) experiencing a greater median wind speed of 2.04 $m\ s^{-1}$ compared to 0.93 $m\ s^{-1}$ at the SW600 site (Fig. 2). The average daily dose, calculated from the three months of particulate monitoring, was consistently higher for the N200 site than for the SW600 site (Table 1). However, particle size was significantly larger ($P < 0.001$) at the further SW600 site than at N200 (0.34 and 0.31 μm, respectively) (Fig. 3).

At both weather stations, winds were mostly from the southwest. And, most of the stronger winds were from the southwest (Fig. 2), although the N200 monitoring station recorded periodic strong winds from the northeast. Both the fall season and the direction of the winds were consistent with Santa Ana winds—the strong

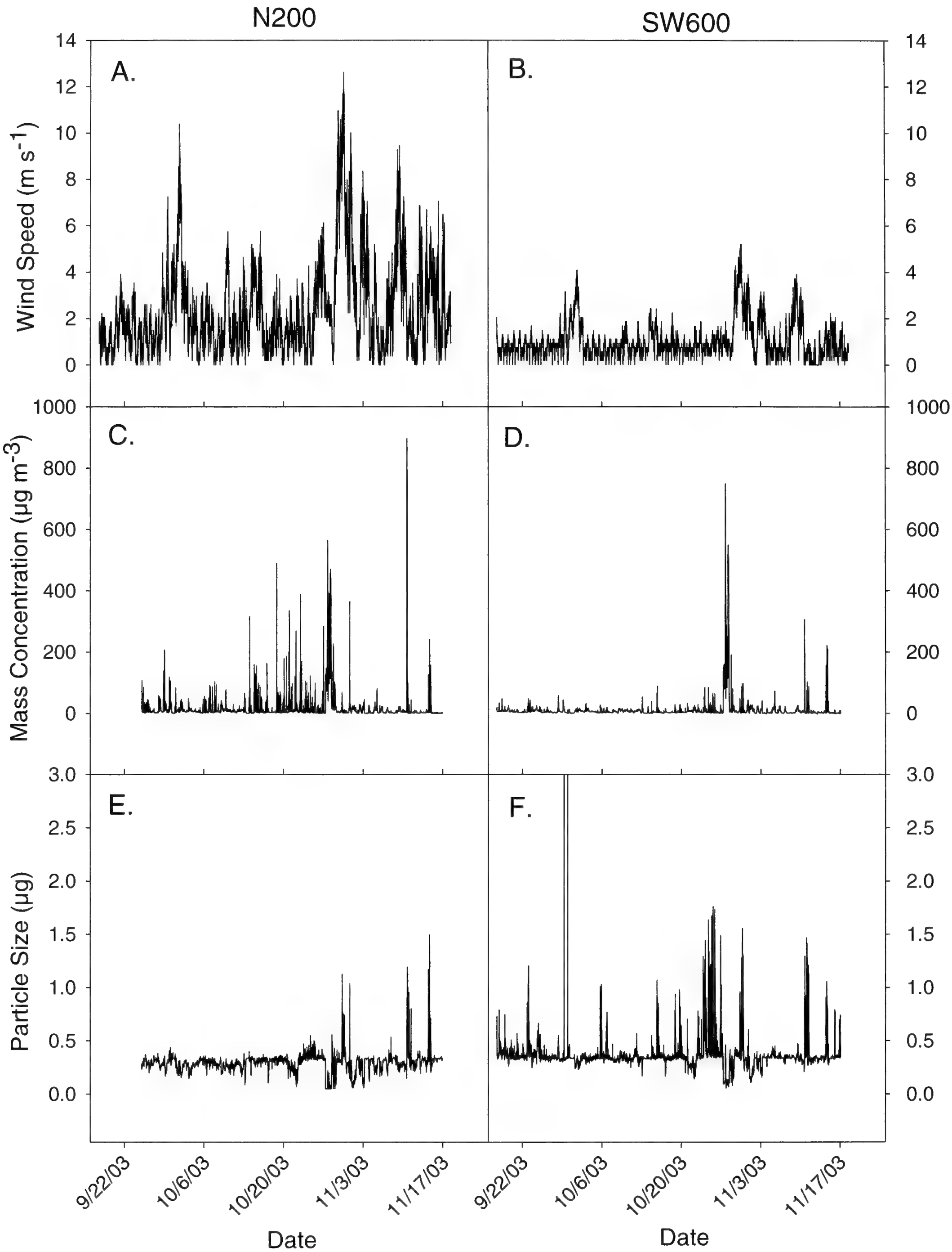


FIG. 3. Comparison of wind speed (panels A and B), atmospheric particulate loads less than 10 µm (panels C and D) and average particle size (panel E and F) between a sampling site adjacent to mining activities and a site partially shielded by juniper forest vegetation.

dry winds that occur in the fall in Southern California. The SW600 monitoring station recorded gentle breezes in all directions. The differences in wind patterns recorded at the two monitoring stations are likely due to topography (see Fig. 1). The SW600 site was located in a relatively open, flat area, whereas the N200 station was installed on an east-facing slope.

Data collected by the DR-4000 particulate monitors at the two locations indicated that wind direction and speed were important for deposition (Fig. 3). Average concentrations of particu-

lates were consistently higher at the N200 station reflecting both proximity to the crusher and prevailing wind directions (Fig. 3A, B), but periodic spikes over 400 μg m^{-3} occurred throughout the fall of 2003. Particulate sizes tended to be small, roughly 0.5 μm diam., but windier conditions increased the average diameters to 1.0 μm (Fig. 3E). The average concentrations at the SW600 location were indicative of lower wind speeds overall (Fig. 3B). Spikes in atmospheric concentration coincided with increased wind speed, and changes in wind direction (Fig. 2). Particle sizes were significantly larger at the SW600 site during these higher wind events.

The amounts of carbonate dust collected in the passive samplers were consistent with the measurements of all aerosols recorded by the DataRam 4000 active monitors. In Fig. 4, the largest concentration of carbonate dust was collected from the N, W, and SW. The data from NW transect were incomplete and not shown. At 200 m these three sampling sites were similar to each other, but significantly greater than the S or SE locations ($P < 0.001$). Consistent with the prevailing wind direction, the N transect collected significantly more $CaCO_3$ at all distances ($P < 0.001$). For all other transects, carbonate dust concentrations were essentially zero by 600 m from the crusher.

Direct deposition to foliage was measured in 2003 (Fig. 5). Foliage collected from the N200 site had significantly ($P < 0.001$) greater $CaCO_3$ at all three sampling periods than any of the other locations. Carbonates measured on foliage collected from N600 and SW400 on Oct 23, 2003 were significantly greater than the deposition measured at the other locations ($P < 0.05$).

Figure 6 shows the wide range of particle sizes collected on foliar surfaces. All four panels are of *Eriogonum microthecum*. Panel B shows the lower surface at 67× magnification. Dust particles are roughly spherical and appear to be trapped in the tread-like trichomes. At higher magnification (1098×), dust particles collecting on the upper surface (panel D) range from less than 1 μm to clumps of material greater than 20 μm. There appear to be at least two types of particles: very angular particles typical of clays and less structured particles typical of calcium carbonates. Both panels C and D capture examples of particles lodged in stomata, at least partially blocking the openings. Note that many of the particles are much larger than the 0.5 μm to 1.0 μm average size determined by the DataRam aerosol monitors.

Deposition of carbonate containing dust had a significant effect on photosynthesis and gas exchange in plants growing under high (N200) and low (SW600) deposition (Table 2). In September 2003, photosynthesis was reduced by 15% and transpiration was reduced by 27% (Table 2).

Reduction in physiological function was reflected in phenology. Total shoot length, foliated length, and length of the new growth were all significantly reduced in plants sampled at the N200 location (Table 3). However, number of stems per plant, number of new branches initiated, and number of flowers per branch did not different across the three locations.

Discussion

Atmospheric deposition. Topography and wind patterns were the primary factors controlling deposition loads at each of the monitoring stations. Secondarily, and much more difficult to capture in this sampling scheme, was the effect of filtering by vegetation. Trees and shrubs are very effective at capturing mining and manufacturing particulates (Zubareva et al. 1999). The four north sampling locations (see Fig. 1) were along a ridge with relatively unobstructed fetches from both the active mine and crusher, as well as unused (but exposed) strip-mines. In contrast, the south and southeast transects were screened by large, old juniper trees, scrub oaks and other native vegetation. This, in part, explains why deposition to the south and southwest transects was lower than one might expect given the wind patterns shown in Fig. 2B.

The passive sampling method only captured material moving vertically; thus, it likely underestimated total deposition to a foliar canopy. Because foliage is an effective screen and because surface roughness tends to enhance deposition, landscape accumulation of dust may have been several times higher than the values estimated from the passive collector cups. Moreover, only carbonates were measured. Therefore, it is likely that the total movement of dust due to the mining operation was considerably greater.

In an extensive study of dust movement in Nevada and Southern California, U.S. Geological Survey scientists determined deposition using an analogous vertical capture system. Fluxes of "total dust" ranged from 5.7 g m^{-2} yr^{-1} to 38.7 g m^{-2} yr^{-1} across 60 arid and semi-arid wildland areas (Reheis and Kihl 1995). Four of their sampling sites were on the western slopes of the San Bernardino Mountains at roughly 1000 m elevation. These sites tended to be in the higher deposition range at 13.7, 17.0, 23.3, and 38.7 g m^{-2} yr^{-1}; much of the source was attributed to Santa Ana winds. The authors also quantified carbonate content, which accounted for 10–15% of total load. Total carbonate deposition in our study was measured for six months and was substantially higher than the

TABLE 1. AVERAGE DAILY DOSE OF TOTAL ATMOSPHERIC PARTICLES MEASURED AT TWO LOCATIONS. N200 was adjacent to the rock crusher and SW600 was partially shielded by juniper forest vegetation.

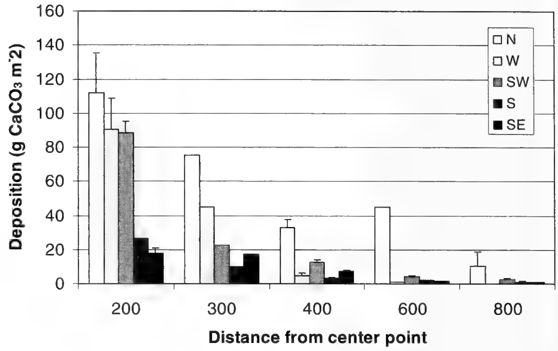
	Days monitored	Average daily load ($mg\ m^{-3}\ d^{-1}$)	
		N200	SW600
Sept	6	12.53	5.46
Oct	31	18.57	13.80
Nov	16	9.04	7.25

Reheis and Kihl data. If we consider the total deposition data published by Reheis and Kihl, as "background" deposition, most of our sampling sites within 400 m of the crusher were well above background, while the sites outside of 400 m (with the exception of the north transect) were at or below background levels. Although sites close to the crusher were clearly affected by mining and transportation activities, some of the more distant sites also appeared to be affected by dust from waste piles and inactive mine areas.

The active monitors measured total suspended particles, regardless of the mineralogy or where they ultimately deposited. The EPA criteria for unhealthful conditions for human exposure is a 65.4 $\mu g\ m^{-3}$ average over 24 hr. There is no criterion standard for adverse effects on ecosystems. There were several health criterion exceedances at the N200 location, and one or two at the SW600 location. When the atmospheric concentration data are calculated as an average daily load (Table 1), the difference between the two sites is relatively small. Suspended particle loads at the SW600 location were 45% to 80% of that measured at the N200 site. However, when the measured deposition to each of these sites is compared, a much larger difference is evident (Fig. 4).

Plants. For the most part, deposition to foliage proved to be an inconsistent monitoring method, although measured quantities did correspond to $CaCO_3$ trapped in the passive samplers, in that the sites with higher deposition as determined by the passive samplers also had higher accumulations on leaf surfaces. One of the reasons for inconsistencies in measurements is the hygroscopic nature of $CaCO_3$. The boundary layer of all living leaves contains a shallow layer against the leaf surface that is saturated with water. Dewfall also partially solublizes carbonate particles causing them to clump, dissolve, blow off, and otherwise affect deposition characteristics of plant surfaces.

Decreases in plant physiological function and growth corresponded to increased deposition rates. This study confirmed the observations reported for *Larrea tridentata* and *Atriplex canescens* in the Mojave Desert (Sharifi et al. 2003), for *Quercus coccifera* in Greece (Vardaka et al. 1995) and for mixed hardwoods in Virginia (Manning 1971). In the study presented by Sharifi et al. (1997), road dust was the source of deposition and estimated surface accumulation



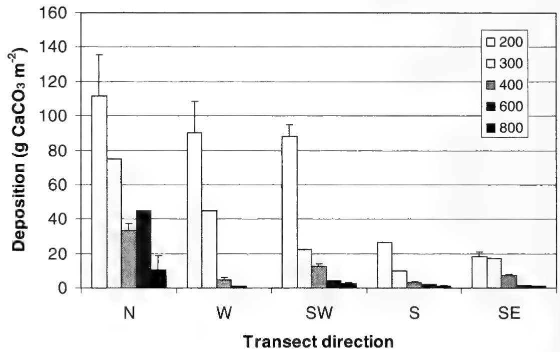


FIG. 4. Sums of carbonate deposition collected by passive samplers during the growing season, April through October, 2004. Samplers were placed along ordinal directions radiating from a center point close to the rock crusher. Samplers were replicated 3 times at the 200, 400 and 600 m distances. The NW transect data was incomplete and is not shown. The E1000 and SW1000 sites are also not displayed.

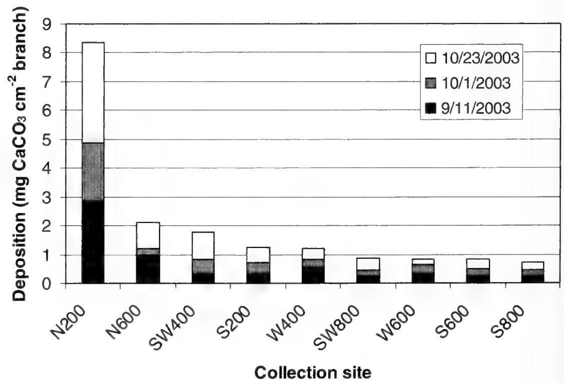


FIG. 5. Dust deposition to *Eriogonum microthecum* foliage during the fall of 2003. Branches were rinsed at the beginning of the experiment and then collected at 3 wk intervals.

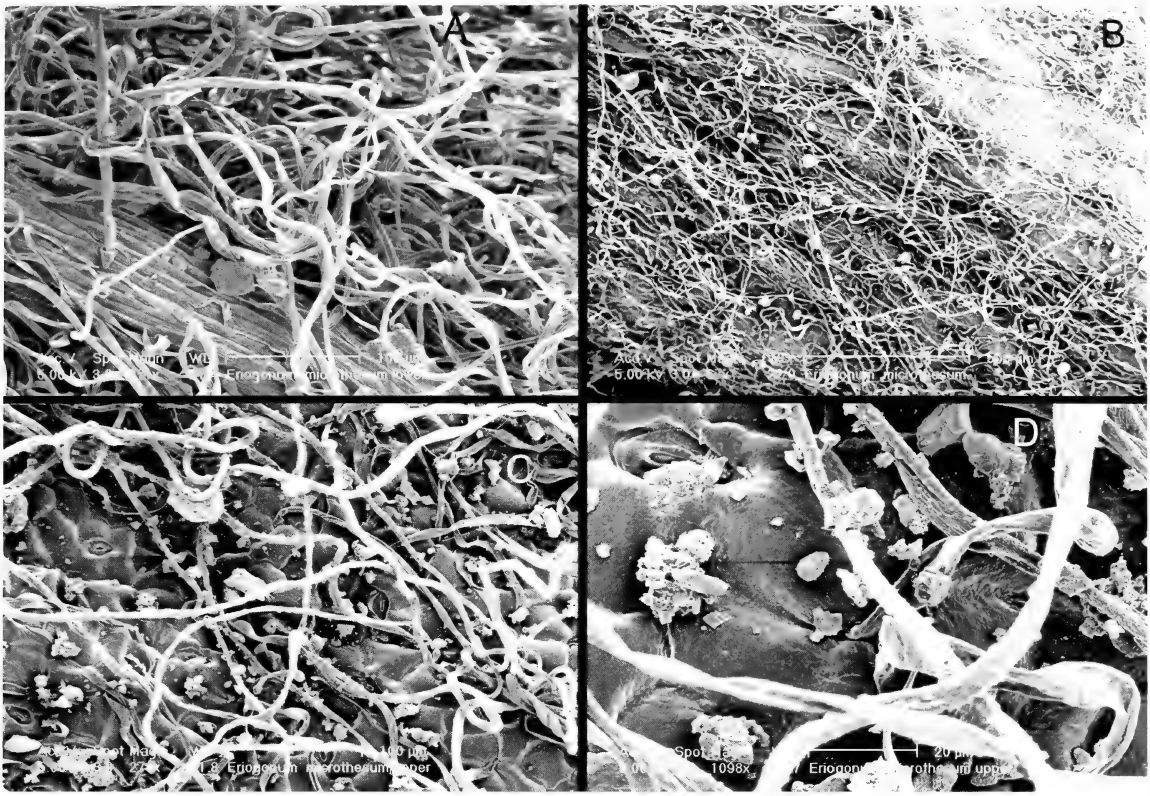


FIG. 6. Scanning electron micrographs of *Eriogonum microthecum* collected from locations near the mining operations. Panel A: 274× magnification, lower surface. Panel B: 67× magnification, lower surface. Panel C: 271× magnification, upper surface. Panel D: 1098× magnification, upper surface. Note stomata on the upper surface.

was 16 g m^{-2} for *Larrea* and 40 g m^{-2} for *Atriplex*, which is similar to the 10 to 20 g m^{-2} of $CaCO_3$ we estimated for *E. microthecum*. Depression in photosynthesis was also quite similar between the two studies. In *Larrea*, CO_2 assimilation rates were 13.2 μmol m^{-2} s^{-1} at the clean sites and 2.3 μmol m^{-2} s^{-1} for the dusty sites. *Atriplex* assimilation rates went from 19.9 μmol m^{-2} s^{-1} (clean) to 12.9 μmol m^{-2} s^{-1} under heavy loads of road dust. The differences in assimilation rates of *E. microthecum* exposed to carbonate dust were smaller than in the desert study, but statistically were significant with a difference of 8.32 μmol m^{-2} s^{-1} at the cleaner location and 7.06 μmol m^{-2} s^{-1} at the dusty location. Similar differences in photosynthetic rates were also reported for *Q. coccifera* by Vardaka et al. (1995) and others (Farmer 1993).

The differences in phenological characteristics exhibited by *E. microthecum* were also consistent with the reported literature. Older studies conducted near a limestone mine in Virginia noted reduced growth in hemlock, wild grape, and sassafras (Manning 1971). Although we did conduct preliminary evaluations of the leaf surface condition of several local plant species, they were less detailed than those by Bačić et al. (1999) who carefully described and monitored the effect of cement factory dust on the epicuticular wax of *Pinus halepensis* needles. Dry and wet deposition of limestone causes serious damage to the needle surfaces and seemed to accelerate blockage of stomatal cavities. Based on our preliminary evaluations, we suspect at our heaviest deposition sites, similar effects are occurring, but conclusive evidence will require further study.

TABLE 2. MEAN GAS EXCHANGE MEASUREMENTS FOR N200 AND SW600 SITES (±1 SE). Letters denote a significant difference between sites ($P < 0.05$).

	Units	N200	SW600	P	F
Photosynthesis	μmol m^{-2} s^{-1}	7.06 ± 0.49[a]	8.32 ± 0.39[b]	<0.001	41.982
Conductance	mol m^{-2} s^{-1}	0.12 ± 0.01[a]	0.16 ± 0.01[b]	<0.001	264.370
Transpiration	mmol m^{-2} s^{-1}	5.24 ± 0.22[a]	7.15 ± 0.33[b]	<0.001	606.142

TABLE 3. PHENOLOGIC MEASUREMENTS OF THREE *ERIOGONUM MICROTHESUM* POPULATIONS AT THREE DISTANCES FROM MINING ACTIVITIES. Ten plants per site were selected and three branches per plant were marked and resampled through the growing season.

		April		June		September	
	Site	Mean (n = 30)	*SEM*	Mean (n = 30)	*SEM*	Mean (n = 30)	*SEM*
No. Stems per plant	N200	10.70	*0.49*	nd		5.89	*1.10*
	SW600	9.40	*0.76*	nd		6.60	*0.79*
	SE1000	11.20	*0.45*	nd		6.00	*0.57*
Total shoot length (base to apex, mm)	N200	129.90	*3.20*	113.45	*5.47*	117.59	*5.11*
	SW600	137.33	*4.52*	147.00	*6.58*	150.86	*7.15*
	SE1000	152.70	*5.94*	163.50	*5.86*	169.50	*5.02*
Foliated shoot length	N200	50.33	*3.13*	70.83	*4.38*	58.89	*4.97*
	SW600	68.63	*4.41*	95.41	*5.84*	79.48	*6.52*
	SE1000	69.07	*3.17*	95.00	*3.47*	93.07	*2.70*
Length of new growth	N200	2.47	*0.24*	52.29	*4.85*	43.31	*4.92*
	SW600	2.77	*0.16*	61.90	*5.03*	58.28	*5.10*
	SE1000	1.87	*0.13*	64.40	*5.95*	60.33	*7.35*
No. New branches per shoot	N200	6.60	*0.31*	4.15	*0.30*	2.48	*0.29*
	SW600	7.87	*0.38*	5.77	*0.51*	2.07	*0.27*
	SE1000	7.83	*0.28*	4.30	*0.32*	2.73	*0.39*
No. flowers per stem	N200	0.00		1.34	*0.13*	0.88	*0.06*
	SW600	0.00		0.70	*0.15*	0.88	*0.06*
	SE1000	0.00		1.40	*0.16*	0.93	*0.05*
Dust deposition g $CaCO_3$ m^{-2} (April through Sept)	N200	0.00		24.67	*3.85*	35.84	*13.77*
	SW600	0.00		4.15	*0.01*	2.66	*0.19*
	SE1000	0.00		1.17	*0.08*	0.44	*0.19*

CONCLUSIONS

The differences in growth and physiology suggest that plants growing within 400 m of disturbed limestone landscape or unprotected stockpiles are in degraded habitats. Plants further away, but in exposed areas within the prevailing winds are also in degraded habitats. Our data using a surrogate species in combination with data from the published literature indicates that deposition of dust, particularly carbonate dust, can reduce productivity of several endangered plant species. We conclude that limestone mining has detrimental effects on endemic populations of these rare species.

Our data suggest three mitigation measures that could reduce the extent of habitat degradation. First, maintain vegetation buffers around the crusher, stock and slag piles, and around the open mining operations. Natural barriers from trees and shrubs provide dust screens that may benefit sensitive species. Second, keep mining activities contiguous and contained. The greater the perimeter, the greater the extent of the disturbance and habitat degradation. Third, cover and replant spent mines, slag heaps, and areas no longer in active use.

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POLLINATORS OF AN ENDEMIC AND ENDANGERED SPECIES, *MAMMILLARIA GAUMERI* (CACTACEAE), IN ITS NATURAL HABITAT (COASTAL DUNE) AND IN A BOTANICAL GARDEN

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ABSTRACT

Mammillaria gaumeri (Britton & Ross) Orcutt (Cactaceae), an endemic plant of the Yucatan Peninsula, is included by the Mexican government in the list of species that require special protection. Its natural habitat is now restricted to fragmented areas and protection programs involve botanical gardens in growing individuals rescued from disturbed areas. Little information is available on the reproductive characteristics of this species and nothing is known of its pollinators. We investigated the visitors of *M. gaumeri* flowers, collecting and observing bee species in its natural habitat (i.e., coastal dune) and in a botanical garden, where coastal dune vegetation had been created. Observations were made on plants whose density was artificially increased by grouping flowering individuals. At each site, we: 1) collected insects visiting the flowers; 2) recorded number of visits; and 3) video-recorded bee movements on the flowers. As expected, the number of bee species and visitation frequency were higher at the botanical garden than at the coastal dune. After landing on a flower, bees either inspected the anthers or dived among them. These behaviors, carried out by all observed species, seemed related to the state of the anthers (full or empty of pollen) and stigma lobes (opened or closed). Specifically, visits lasted longer when anthers were full of pollen and stigma lobes were opened. The same bee species recorded on the dune were also recorded at the botanical garden, suggesting that the artificial dune at the botanical garden offered suitable conditions for the natural pollinators of this endangered cactus.

RESUMEN

Mammillaria gaumeri (Britton & Rose) Orcutt (Cactaceae) es endémica de la Península de Yucatán y está incluida en la lista de especies que requieren protección especial por decreto del gobierno de México. Presenta un hábitat restringido en áreas fragmentadas y los programas de protección consideran el rescate de individuos de áreas perturbadas para crecerlos en jardines botánicos. De la poca información disponible sobre las características reproductivas de esta especie, no se conoce nada de sus polinizadores. En este estudio, nosotros investigamos los visitadores de las flores de *M. gaumeri* y observamos y colectamos las especies de abejas en su hábitat natural (duna costera) y en un jardín botánico, donde el hábitat de la duna costera ha sido imitado. Las observaciones fueron hechas en plantas cuya densidad fue aumentada artificialmente con varios individuos en floración. En cada sitio: 1) colectamos los insectos que visitaron las flores; 2) registramos el número de visitas; y 3) filmamos los movimientos de las abejas sobre las flores. Como esperábamos, el número de especies de abejas y la frecuencia de visitas fueron mayores en el jardín botánico que en la duna costera. Al aterrizar sobre una flor, las abejas se comportaron de dos diferentes maneras: ya sea que ellas inspeccionaban las anteras o se zambullían entre ellas. Estos comportamientos, realizados por todas las especies visitadoras, parecen estar relacionados con el estado de las anteras (llenas o vacías de polen) y a la posición de los lóbulos del estigma (abiertos o cerrados). Específicamente, las visitas duraron más tiempo cuando las anteras estaban llenas de polen y los lóbulos de los estigmas estaban abiertos. Las mismas especies de abejas se colectaron en ambos sitios, lo que sugiere que la duna artificial del jardín botánico también ofrece condiciones adecuadas para los polinizadores naturales de este cactus amenazado.

Key Words: botanical gardens, Cactaceae, endangered cactus, endemic cactus, *Mammillaria gaumeri*, pollinators.

When dealing with the conservation of endangered plant species, research usually has focused on habitat preservation (Hall and Gillespie 2004), reserve design (Deltoro et al. 2004), demography for short-term population management (Fox and Gurevitch 2000), and the possibility of reproduction in botanical gardens for future reintroduction in their natural range of distribution (Perini and Tornadore 2004). But, it is also frequently

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reported that endangered plant species experience reproductive failure that may be strongly related to the loss of pollinators (Aronne and Wilcock 2004). Many species may vegetatively reproduce, especially when pollinators are rare or absent and flower fertilization is low. However, pollination (i.e., cross-pollination) of flowering plants provides the enormous benefit of gene flow in the population and helps to maintain the species' ability to respond to a changing environment (Proctor et al. 1996; Price 2002).

To formulate effective strategies for management and conservation, it is essential to understand the ecological and evolutionary nature of plant-pollinator interactions. Notwithstanding that pollinators of many plant species are not yet identified (Kearns et. al. 1998), there is already evidence that a deficit of pollinators in fragmented habitats threatens plant populations and plant diversity (Lennartsson 2002).

Regarding plant conservation and reintroduction, one potential problem is that some native pollinators may have disappeared. Nonetheless, most flowering plants are pollinated by moderate to high numbers of insect species, and most floral visitors usually visit many different hosts (Corbet 1997; Kearns et al. 1998). Thanks to the multiple pollinators observed for the majority of plant species, "new" pollinators might adopt a plant if its original pollinators are absent. The adoption of endangered species by alternative pollinators may also be crucial when trying to propagate them under artificial conditions, as in botanical gardens. Thus, priorities for research programs should include the identification of native pollinators as well as other possible pollinators of the threatened plant species.

Mammillaria gaumeri (Britton & Rose) Orcutt (Cactaceae, tribe Cacteae) is a globular cactus endemic to the northern coast of Yucatan. This species is under special protection in the Protection of Natural Resources Document by the Mexican government (NOM-059-ECOL-2001). It grows only in some restricted areas, due to fragmentation of its natural habitat by human disturbances such as urbanization, cattle-range management, and agriculture (Durán et al. 1998). Some studies deal with its distribution and abundance, seed germination, and seedling survival (Leirana-Alcocer and Parra-Tabla 1999; López-Jiménez 2001; Cervera et al. 2006), but accurate information on its reproductive biology is still lacking. Our aim was to identify the native pollinators of this rare species, through the collection of pollinators in one of its natural habitats, the coastal dune scrubland. We were also interested in the flower visitation rate in a botanical garden, where plants rescued from disturbed areas have been preserved on an artificial dune. Between these two sites we compared pollinator species and visitation frequency. We described the bees' behavior to infer each species' interest in the resources offered by the flower and possible elements crucial in flower selection by pollinators.

Methods

We conducted field observations on a natural population of *Mammillaria gaumeri* in the coastal dune scrubland of San Benito (21°19′10″N, 89°30′40″W) and in an artificial coastal dune recreated at the Centro de Investigación Científica de Yucatán (CICY) Botanical Gardens in the city of Mérida (21°02′38″N, 89°38′22″W). The subject of the study is a small globular cactus that grows on exposed areas as well as under cover of vegetation.

At the two sites, the micro-habitats were very similar, but differed in the respective surroundings. On the coastal dune, the vegetation was mainly characterized by small bushes and succulents that can reach heights from 3 to 5 m, and common species were *Coccoloba uvifera* (L.) L. (Polygonaceae), *Cordia sebestena* L. (Boraginaceae), *Bravaisia berlandieriana* (Nees) T.F. Daniel (Acanthaceae), *Agave angustifolia* Haw. (Agavaceae), *Opuntia dillenii* (Ker Gawl.) Haw. (Cactaceae) *Acanthocereus tetragonus* (L.) Hummelinck (Cactaceae) and *Myrmecophila tibicinis* var.*christinae* Carnevali & Gómez-Juárez (Orchidaceae); the area surrounding the dunes included urban areas and natural vegetation. The CICY Botanical Garden recreates many habitats on an area of 27,000 m^2, and maintains 107 families and 592 plant species. Around it, land was urbanized.

We established a 2-m × 2-m observation area at each site. At San Benito, where we located about 4 flowering individuals of *M. gaumeri* on the dunes in open areas, 7 plants growing in pots were added. Plant density at this study site was 0.86 individuals per m^2, so density was increased to 2.75 m^{-2}. At CICY Botanical Gardens, 9 plants were growing in pots and located in open areas (plant density = 2.25 m^{-2}). Flower density was then increased compared to natural conditions, but kept constant at both sites (about 15 opened flowers during observations).

We collected specimens and made observations during the early dry season (January 27 to February 3, 2005), which lasts from November to February and is marked by an alternation of full sun and cloudy days, with infrequent precipitation and strong winds. Because Hymenoptera are often inactive on cloudy days, we used data from sunny days only. Status of flowers (open/closed) was recorded every hour for nine flowers on four plants.

Considering weather conditions (around midday clouds appeared) and flower opening, we based comparisons on visitation frequency between 10:30 and 12:00. The number of flower-

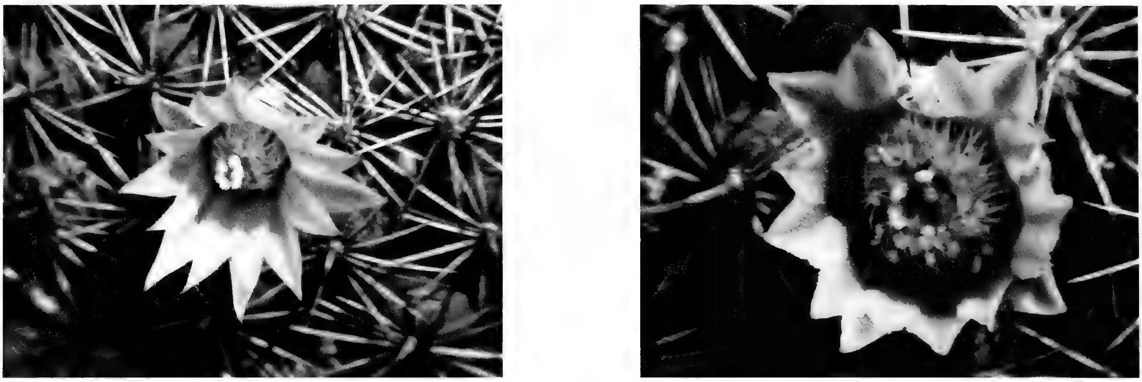

FIG. 1. Flowers of *Mammillaria gaumeri*. The anthers are curved towards the stigma; the lobes are still close in the flower on the left and open in the flower on the right.

visiting bees was recorded during one day at each site; attention was directed to bees landing independently on each flower by only one observer at each site. Temperature and relative humidity were also recorded during observations, using a digital thermo-hygrometer (Deltha Ohm, HD201-1; Italy).

The video-recording of some visits (n = 31) with a digital video-camera (Sony, DCR-TRV80E; Japan) equipped with magnifying lens provided data on: landing surface elected by the bee; flower characteristics at the moment of the visit (empty/full anthers, open/closed stigma lobes); bee behaviors on the flower; and visit duration. Video-recording was done on January 27, 29 and February 3, 2006 only when bees were approaching flowers. Total duration of the video record was about 30 min, obtained during 9 hr of observations.

Due to difficulties of identification related to their small size, bees were divided into three recognizable classes: small black bees, megachilid bees, green bees. Additionally, some scattered observations at both sites and specimen collection were done, on sunny days, from January 15 to February 10, 2005.

Statistical analysis was performed using Statistica (StatSoft Inc., Tulsa, Oklahoma, USA) and following Zar (1974).

RESULTS

Characteristics of *Mammillaria gaumeri* Flowers

The flowers of this species are of a pale color, with whitish-yellow petals and light yellow anthers. Anthers are very numerous and curved towards the stigma (Fig. 1). The stigma has four lobes that changed in color from yellow to reddish-pink and from a closed to an open stance. Flowers were fully open (Fig. 2) during the central hours of the day (12:30–15:30). However, we observed bees entering flowers with petals only slightly opened.

Number of Bee Species

Table 1 reports all species collected at the two sites. We collected two species at San Benito: an Apidae, *Ceratina* Latreille sp. 1, and a Colletidae, *Hylaeus quadratifera* (Cockrell). Also, we observed an ant, which apparently inspected a flower, and we saw a winged wasp (possibly a Sphecidae or a Mutillidae) visiting a flower.

We collected five bee species at CICY Botanical Gardens. Among them, there was one of the bee species collected at San Benito (Colletidae, *Hylaeus quadratifera*), another Apidae belonging to the genus *Ceratina* Latreille sp. 2, and other three species belonging to two families (Megachilidae, *Megachile* Latreille sp.; Halictidae, *Dia-*

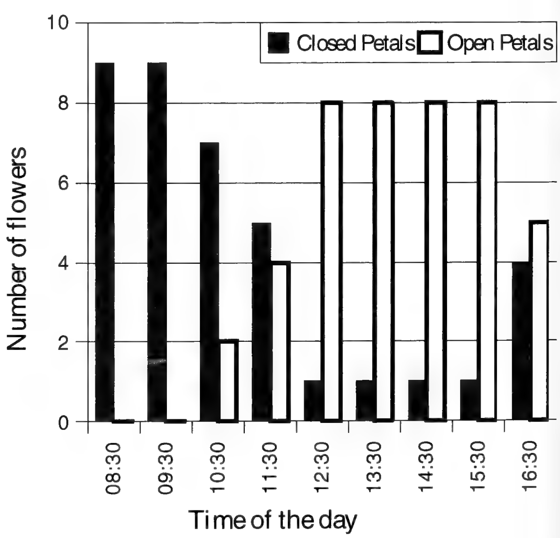

FIG. 2. Opening time of the nine flowers under observation on a sunny day.

TABLE 1. BEE SPECIES COLLECTED DURING OBSERVATIONS ON FLOWERS OF *MAMMILLARIA GAUMERI*. Classification following Michener (2000).

Family	Subfamily	Genus	Species	SAN BENITO	CICY Botanical Gardens
Apidae	Xylocopinae	*Ceratina* Latreille, 1802	Unknown 1	Present	—
			Unknown 2	—	Present
Colletidae	Hylaeinae	*Hyleaus* Fabricius, 1793	*quadratifera* (Cockrell)	Present	Present
Halictidae	Halictinae	*Dialictus* Robertson, 1902	Unknown	—	Present
		Augoclora Smith, 1853	Unknown	—	Present
Megachilidae	Megachilinae	*Megachile* Latreille, 1802	Unknown	—	Present

lictus Robertson sp. and *Augochlora* Smith sp.). During observations, no ant or wasp visited the flowers, although some were present at the site.

Observed species correspond to the bee classes as follows: Small black bees = *Ceratina* sp. 1, *Ceratina* sp. 2, *Hylaeus quadratifera; Dialictus* sp.; Megachilid bees = *Megachile* sp.; Green bees = *Augochlora* sp.

Visitation Frequency

At both sites, climatic conditions during observations were optimal for bee activity, with full sun and high temperatures. At San Benito, temperatures were lower (range 27.0–29.1°C) than at CICY Botanical Gardens (32.0–34.7°C); relative humidity was higher at San Benito (64.3–67.9%) than at CICY Botanical Gardens (36.9–45.1%)., the number of visits recorded at CICY Botanical Garden was 2 times higher than that recorded at San Benito (X^2 = 5.32, P < 0.05). While in San Benito small black bees were responsible for all the visits (n = 16), at CICY Botanical Garden they made 27 out of 32 visits (84%). The other visits were distributed among megachilid bees (3 visits) and green bees (2 visits). (These observations were very limited, however [from 10:30 to 12:00, one day per site].)

Description of Visits

The following descriptions regard the behavior of *Ceratina* sp. 1, *Ceratina* sp. 2, *Hylaeus quadratifera*, and *Megachile* sp.

Bees landed on the flower rapidly: in 69.3% of the cases (n = 26), they landed mainly on the petals and walked to the anthers; in 19.2% of the cases, they landed on the stigma lobes, then move to the anthers, whereas in 11.5% of cases, they landed directly on the mass of anthers. Petals were the more frequent landing surface (X^2 = 15.46, P < 0.001). After reaching the anthers, pollinators a) inspected them with their antennae (42% of cases; n = 31), or b) dove immediately among them (42%), and in a few cases, we recorded c) both behaviors (16%). No statistical differences among the frequency of the three behaviors emerged (X^2 = 4.13, n. s.).

Mean and SE of visit duration of each case is reported in Table 2. The first strategy (i.e., inspecting the anthers) consisted of very short visits: bees landed on the flower as described above and quite immediately flew away. The second strategy (i.e., diving among anthers) included the bee disappearing under the anthers, a lapse of time during which movements were perceived from oscillation of anthers and stigma,

TABLE 2. DESCRIPTIVE STATISTICS OF VISIT DURATION. Observations based on: bee behavior, flower characteristics (anthers and stigma lobes), and bee group. Data obtained from analysis of video-recorded images. Statistical analysis between groups is reported in the text.

	Average (seconds)	SE (seconds)	N
Bee behavior			
inspecting	2.18	0.50	11
diving	11.08	1.39	13
Anthers characteristics			
full of pollen	3.08	0.80	13
empty of pollen	9.87	1.43	16
Stigma lobes characteristics			
opened	9.35	1.44	17
closed	3.25	0.84	12
Bee group			
megachilid bees	8.60	3.44	5
small black bees	6.46	1.10	24

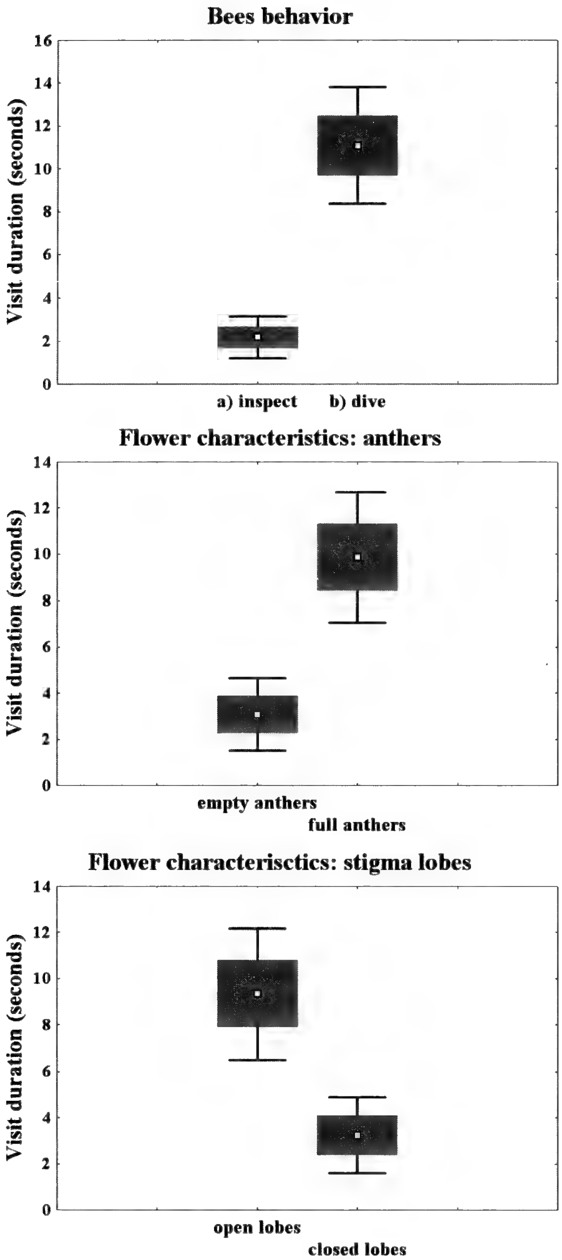

FIG. 3. Average duration of visits depending on bee behavior and floral characteristics (anthers and stigma lobes). Data were obtained from analysis of video-recorded images. Upper graph: visit duration depending on behavior; middle graph: visit duration depending on anthers (full or empty); lower graph: visit duration depending on stigma lobes (opened or closed). Data are means (open squares) ± SE (gray squares) ± 1.96 × SE.

and partial visualization of the bee among the stamens. After that, they emerged and cleaned/moved pollen grains to the legs, possibly resting for a few seconds, while lying on the anthers or on the petals, and then they flew away. The difference in visit duration between the two behaviors was statistically significant (Mann-Whitney z adjusted = −4.186, n 1 = 11, n 2 = 13, $P < 0.001$; Fig. 3, upper graph). There also was a significant difference between visits to flowers with full or empty anthers (Mann-Whitney z adjusted = −3.454, n 1 = 13, n 2 = 16, $P < 0.001$; Fig. 3, middle graph) and with opened or closed stigma lobes (Mann-Whitney z adjusted = 2.996, n 1 = 17, n 2 = 12, $P < 0.005$; Fig. 3, lower graph). When lobes were opened, flowers received 58.6% of visits (n = 29); when stigma lobes were closed, flowers received the 41.4% of visits. In 16 out of 25 visits, the body of a small black bee touched the stigma lobes, while it happened in 4 out of 5 visits for megachilid bees.

DISCUSSION

This preliminary study identified some of the pollinators of an endangered and endemic cactus of the Yucatan Peninsula, both in its natural habitat and in a botanical garden, where its habitat conditions were recreated. *Mammillaria gaumeri* can flower many times during a year, a trait shared with other, more common species of *Mammillaria* (Bowers 2002). Flowering several times within a year may increase the probability of pollination by enabling flowers to encounter pollinators under different environmental conditions.

Ceratina species, as well as *Hylaeus quadratifera* and *Dialictus* sp., accounted for most visits to *Mammillaria gaumeri* flowers at both sites. The tribe Ceratinini (Apidae, Xylocopinae) consists of small and slender species, similar to the worldwide subfamily Hylaeinae (Colletidae), a group of minute to moderate-sized, mostly slender bees with a limited yellow or white mark on the face (Michener 2000). *Ceratina* usually nest in dead plant material, such as hollow or pithy stems or burrows made in rotten woody vines or stems. As do many Allodapinae in the Old World Tropics and *Hylaeus*, they tolerate exposure and highly variable nesting temperatures (Roubik 1989). Michener (1970) found more nests of *Ceratina* in the introduced plant species of gardens than in normal vegetation, which may account for the ability of this genus to invade non-natural areas and consequently provide the pollination service needed.

The two species (*Ceratina* sp. and *Hylaeus quadratifera*) collected on the dune scrubland were the only flower visitors during observations. On the dune, the vegetation provides plenty of nesting substrate (dead plant material). We can imagine that in such an environment a strong relationship between a pollinator and this plant species may exist (flowers are small, pale, located at surface level, often hidden by other plants). Both bee species are characterised by a small size

(four to six millimetres long) and by the fact that pollen is carried in the crop moistened with nectar. This feature may justify the observed behaviour on the flowers: bees diving among anthers may be searching for the nectaries. Nectar is even the main resource found in Hylaeinae nests, so accurate measurement of nectar crop in *M. gaumeri* population may indicate its importance as a nectar resource for the corresponding population of bees. The percentage of individuals observed touching the stigma (64%; n = 31), as well as the ones landing on it, accounts for a potentially good pollination service.

The simulated coastal dune habitat at CICY Botanical Gardens (about 30 km from San Benito) has favored the establishment of the bees found on the dune. At CICY Botanical Gardens many different habitat have been created, such as tropical dry deciduous forest, dry deciduous forest with columnar cacti, and coastal dune scrubland; the high amount of flowering species may also attract more bee species. This is actually confirmed by the bee collection on *M. gaumeri* made at this location and by the significant higher visitation rate recorded compared to the natural coastal dune in San Benito. Again more information on *M. gaumeri* resources may explain such a high rate of visit, considering the diverse flowering plants present at the site and the possible competition among them.

Megachilidae are famous for collecting pollen on the underside of the abdomen. They do not line their cell, but use building materials as lead or petal pieces, chewed leaf pulp, hairs, nectar, resin, pebbles, mud and combinations of these (Michener 2000). Provisions are not shaped in any form, but pollen is loose; some species are pollen specialist (Roubik 1989). They are bigger than *Ceratina* and *Hylaeus* and this may result a disadvantage for the flower because bee movement among the anthers may damage the tissues. Also, considering that in their cells the only provision is pollen, it would be interesting to verify whether these bees were feeding on the nectar or collecting pollen when diving among the anthers. Halictinae includes some of the commonest bees; they mainly nest in the soil, in banks or flat soil, or rarely in rotting wood (but *Augochlora* females do). Provisions are usually firm, sub-spherical and lie on the ventral surface of the cell. The majority of species are polylectic (Michener 2000). Few individuals belonging to these two families have been recorded, but they are probably more widespread than supposed. It would be especially interesting to compare the collection habits of these bees with those species observed on the dune, to estimate their potentiality as pollinators of *M. gaumeri*. In fact, the intensity or quality of pollination may be affected if pollinator species changed (Corbet 1997).

Although there were some differences in foraging and nesting characteristics, all species performed different behaviors depending on the state of the anthers, as well as that of the stigma lobes. These differences highlight the importance of recognition by individual bees of the flower status and possibly also of the reward to be found in the flower. Flower attributes need to be further studied in order to infer the information obtained by the approaching bees and for a better understanding of bee reactions when landing on a flower. This was only a preliminary work, but its results have raised many questions related to the recovery of the natural populations of *M. gaumeri* and its pollinators, and its cultivation in botanical gardens.

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POLLINATION BIOLOGY OF *SILENE LEMMONII* (CARYOPHYLLACEAE), A MONTANE PERENNIAL HERB

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ABSTRACT

Silene lemmonii S. Watson (Caryophyllaceae) is a tap-rooted herbaceous perennial that grows in montane habitats throughout California and Oregon. In 1999 and 2000, I studied the pollination biology and mating system of a single *S. lemmonii* population occurring near Dubakella Mountain in the Trinity National Forest, CA. Although *S. lemmonii* is self-compatible, individual flowers are strongly protandrous and fruit set rarely resulted from autogamy in both years of the study. *Silene lemmonii* flowers bloom at night, yet I observed no nocturnal insects visiting flowers in 1999 and visitation by diurnal bees and flies was infrequent during both years of the study. Despite the paucity of visitors, plants exhibited relatively high fruit set ($\bar{x} = 40\%$ in 1999 and $\bar{x} = 61\%$ in 2000). In 2000, I conducted an experiment to reconcile the occurrence of relatively high fruit set with rare insect visitation. I examined the contribution of insect visitation, autogamy, and jostling-induced geitonogamy (occurring when individual flowers on the same plant brush into one another) to fruit production. I found that fruit and seed production in *S. lemmonii* was primarily mediated by diurnal and nocturnal insect visits, but jostling-induced geitonogamy contributed to ~20% of fruit set. To my knowledge, this is the first study to report jostling-induced geitonogamy and the first to describe the pollination biology of *S. lemmonii*.

Key Words: Caryophyllaceae, geitonogamy, jostling-induced geitonogamy, nocturnal pollination, pollination, pollination syndrome, self-pollination, *Silene*.

The immobile nature of flowering plants makes most species dependent on animal pollinators to carry genetic material to and from potential mates. To attract pollinators, many flowering plants invest considerable resources in pollen and nectar production. However, visitation by animal pollinators can be erratic and unpredictable (Horvitz and Schemske 1990; Fenster and Dudash 2001; Price et al. 2005). Insufficient pollination caused by low visitation limits maternal reproductive success in many species (Burd 1994; Dudash and Fenster 1997; Ashman et al. 2004; Hampe 2005).

Two known alternatives to animal pollination include wind pollination (anemophily) and self-fertilization by autogamy (pollen transfer from anther to stigma within a single flower). Anemophilous flowering plants, such as grasses and oaks, possess several traits (e.g., unisexual, pendant flowers) that facilitate the transfer and receipt of pollen on wind currents (Proctor et al. 1996). While uncommon among species with flowers adapted to attract insect pollinators (entomophily), wind pollination can contribute to fruit production in entomophilous flowers occurring in windy areas (Gómez and Zamora 1996; Norman et al. 1997; Goodwillie 1999). Autogamy occurs in numerous self-compatible taxa (Barrett 1998; Goodwillie et al. 2005), including many species in the genus *Silene* (Lesica 1993; Jürgens et al. 1996; Kephart et al. 1999; Buide and Guitian 2002; Keller and Schwaegerle 2006).

Geitonogamy (transfer of self-pollen between flowers on the same plant) caused by insects visiting multiple flowers on the same plant is well known (de Jong et al. 1993; Harder and Barrett 1995; Hodges 1995; Karron et al. 2004). However, another form of geitonogamous self-pollination –jostling-induced geitonogamy– may occur when self-compatible plants bear more than one flower. If wind causes adjacent flowers on the same plant to jostle into one another, pollen from one flower may move to another receptive stigma on the same plant.

The genus *Silene* (Caryophyllaceae) contains animal-pollinated species that vary in their pollination biology (e.g., Jürgens et al. 1996; Talavera et al. 1996; Brown and Kephart 1999; Buide 2006; Kephart et al. 2006). Several species possess red, day-blooming, hummingbird-pollinated flowers (Menges 1995; Fenster et al. 2006), whereas others have pale, night-blooming flowers that are pollinated by noctuid or sphingid moths (Pettersson 1991; Young 2002; Barthelmess et al. 2006; Kephart et al. 2006). *Silene lemmonii* S. Watson is a pale-flowered, night-blooming species whose pollination biology was relatively unknown prior to this study.

The objectives of this investigation were to study the pollination biology of *S. lemmonii*,

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determine the relative importance of diurnal and nocturnal pollination, and evaluate the relative importance of biotic and abiotic pollination. *Silene lemmonii* has protandrous flowers, wherein each flower appears to shed pollen prior to stigma receptivity. Preliminary observations revealed that insect visits to *S. lemmonii* occurred during the day, while its petals were withered. Furthermore, insect visitation appeared uncommon, yet fruit set seemed relatively high. Since even slight breezes can blow *S. lemmonii*'s glandular-hairy inflorescences into one another (A. Hove, *personal observation*) and flowers in the male and female phases of development frequently occur in close proximity on the same plant, I hypothesized that jostling-induced geitonogamy could contribute to fruit production.

In 1999 and 2000, I conducted a series of observational and experimental studies to address the following questions: (1) Which insect taxa visit *S. lemmonii*?; (2) What fraction of insect pollination occurs during daylight hours compared to twilight and evening hours?; (3) What is the timing of the male (pollen-shedding) phase relative to the female (stigma-receptive) phase within individual flowers?; (4) Is *S. lemmonii* self-compatible? If so, does autogamy occur under natural conditions?; and, (5) During the 2000 flowering season, to what extent does jostling-induced geitonogamy contribute to fruit set and seed set?

Methods

Study Species

Silene lemmonii is a tap-rooted herbaceous perennial found in oak woodlands and coniferous forests of mountain ranges in southern Oregon (Kozloff 2005) and throughout California, including the Klamath Range, Santa Cruz Mountains, Sierra Nevada Range, and Transverse Ranges (Hickman 1993). The vegetative plant body has low-growing stems and its growth form ranges from creeping to erect. When in flower, plants appear much taller (between 40–70 cm), displaying pendant flowers arranged in cymose inflorescences with elongate rachises (Fig. 1). The inflorescence rachises remain smooth while flowers are in bud and then become sticky with glandular hairs as the flowers begin to open. During the flowering season, adjacent inflorescence rachises on an individual plant sometimes stick to one another (A. Hove, *personal observation*).

In 1999, each plant bore an average of 8.2 inflorescences (n = 130 plants), which displayed two to four open flowers throughout the flowering season (A. Hove, unpublished data). Thus, the average number of open flowers per plant at a given time during the flowering season typically ranged from approximately 16 to 32. Plants varied greatly in flower production, with small plants bearing one flower and the largest plants bearing nearly 70 flowers. On average however, individuals produced 20.5 flowers per plant (n = 70, SE = 1.97) during a flowering season.

Silene lemmonii flowers have no detectable fragrance and produce little to no nectar (A. Hove, unpublished data). The yellowish-white to pale pink petals wither during the heat of midday and then unfold at dusk, remaining expanded into the evening and early morning hours. Stigmas appear receptive and anthers display copious amounts of pollen during both the daylight and evening hours.

Study Site

In 1999 and 2000, I studied a large population of *S. lemmonii* growing near Dubakella Mountain in Trinity County, California. The site is located in the Trinity National Forest approximately 32 km southeast of Hayfork. At the site, *S. lemmonii* was abundant in the herbaceous understory within the mixed coniferous forest. The flowering season began in late May–early June and ended in early July. Wind speeds recorded during the 2000 flowering season did not exceed 8 kph ($\bar{x}$ = 0.97 kph, SE = 0.12).

Identification of Floral Visitors and Their Visitation Rates

To identify insect visitors, determine their corresponding visitation rates, and ultimately estimate the number of visits a flower receives during its lifetime, I established four observation stations in 1999 and five stations in 2000. I placed the observation stations at least 150 m apart from one another at various locations in the population. At each station, I tagged all plants whose flowers could be easily monitored without the aid of binoculars by an observer sitting approximately 1.5 m away from the plants.

Field workers conducted hour-long observations throughout both flowering seasons during the following time periods: morning (sunrise–1200), afternoon (1200–1800), twilight (1800–2100), and night (2100–sunrise). For night observations, two people worked together, using red lights to view floral visitors. In 2000, field workers recorded wind speed with an anemometer approximately every 20 min for the duration of each observation period.

When insects visited flowers, field workers recorded visitor identity, number of flowers visited, the gender-phase of each flower visited, and whether the insect foraged on nectar or pollen. Visitors were captured for identification if possible. I observed 26 plants for a total of 16 hrs in 1999 and 57 plants for a total of 20 hrs

FIG. 1. Drawing of a *Silene lemmonii* plant. Copyright provided by the artist, Alex Yelich.

in 2000. Observation periods were distributed evenly across plants during both years of the study.

Visitation rates (# insect visits $flower^{-1}$ hr^{-1}) were calculated for each visiting insect taxon. Because of infrequent insect visitation in 1999 and 2000, I also calculated a pooled visitation rate (# visits by all insect taxa $flower^{-1}$ hr^{-1}) for each year. I estimated the number of open flowers per plant by multiplying the mean number of inflorescences per plant and the mean number of open flowers per inflorescence (n = 130 plants).

In both years, I estimated the total number of visits a flower receives over its lifetime as the product of the pooled visitation rate and the average number of hours a flower stays in bloom (216 hrs in 1999 and 118 hrs in 2000). My estimates of total visit number depend on several parameters, most of which are themselves estimates: the number of inflorescences per plant, the number of flowers per inflorescence, and floral lifespan. To evaluate the sensitivity of calculated visitation rates and expected floral visits to changes in estimated parameters, I conducted two sensitivity analyses by varying the magnitudes of two of these parameters (number of open flowers per plant and floral lifespan) and examining the subsequent effect of each of these changes on the pooled visitation rate and expected visit number per flower.

Comparison of Diurnal versus Nocturnal Insect Pollination

During both field seasons I conducted an experiment designed to evaluate the relative

contribution of diurnal and nocturnal insect pollination to fruit and seed production. I used cages made of window-screening mesh (with 1.4 mm × 1.6 mm openings) to exclude pollination by either diurnal or nocturnal visitors. I assigned each plant in this experiment to one of the following three treatments: *i.* caged from sunrise to sunset and exposed to potential pollinators during the twilight and nighttime hours (hereafter referred to as "night"); *ii.* caged from sunset to sunrise and exposed during the day; or *iii.* uncaged and exposed to potential diurnal and nocturnal pollinators for the entire flowering season. The uncaged plants served as a control group, allowing me to assess the total amount of fruit and seed production resulting from both diurnal and nocturnal pollination.

In 1999, I randomly selected 105 plants throughout the population. I made 20 plants available only to nocturnal pollinators and I made 20 plants available only to diurnal pollinators. Sixty-five control-group plants remained uncaged and accessible to both diurnal and nocturnal pollinators throughout the flowering season. In 2000, I randomly selected 120 plants from the population. I caged 40 plants at night, leaving them exposed during the day. I also caged 40 plants during the day and exposed them at night. I assigned 40 plants to the control group.

At the end of both field seasons, I collected all mature fruits on the plants, stored them individually in coin envelopes, and dried them at 110°C for four days. Fruits typically contained seeds that appeared viable (hereafter referred to as "viable"), filled ovules, and unfertilized ovules, all of which were visually distinguished from one another with a dissecting microscope (*sensu* Kephart et al. 1999). Large and plump seeds, with furrowed reddish-brown seed coats, were considered viable. Filled ovules were smaller than viable seeds, flattened, and lacked well-developed seed coats. Both viable seeds and filled ovules were easily distinguishable from the much smaller and flatter, presumably unfertilized ovules. In 1999 and 2000, I assessed seed set by counting the number of viable seeds per fruit.

In 1999 and 2000, I compared mean fruit set (number of fruits produced/total number of flowers per plant) among the three treatment groups with one-way ANOVAs followed by Fisher's LSD Multiple Comparison Tests. I also used one-way ANOVAs and Fisher's LSD Multiple Comparison Tests to compare mean seed set among the three groups for both years of the study. I removed 45 plants in 1999 and 47 plants in 2000 from the analysis because of mortality resulting from either anther smut disease or herbivory (to evaluate the distribution of these removals across treatments, refer to actual sample sizes presented in Table 3).

Timing of the Male and Female Phases of Floral Development

In 1999 and 2000, I randomly selected plants from the population and daily monitored four flowers per plant. I observed 15 plants in 1999 (n = 60 flowers) and 10 plants (n = 40 flowers) in 2000. For each flower, I noted the duration of its male phase as well as its female phase. I considered flowers to be male once anthers began to release fresh pollen until all the anthers withered. The female phase commenced when stigmas appeared moist and papillate, lasting until the styles began to wither. In 1999, I conducted hydrogen peroxide tests (Kearns and Inouye 1993) on 20 moist-papillate stigmas to confirm their receptivity and my ability to visually identify a flower's female phase.

Degree of Self-compatibility and Capacity for Autogamy

To determine *S. lemmonii*'s degree of self-compatibility, I randomly selected and caged 20 plants in 1999 and 40 plants in 2000. To prevent pollination by visiting insects and browsing by deer, plants remained caged until fruit maturation occurred.

I randomly assigned 15 female-phase flowers on each plant to one of three possible hand-pollination treatments: *i.* addition of self-pollen (pollen from a male-phase flower on the same plant); *ii.* addition of pollen from two distant plants; or *iii.* unmanipulated (no supplemental pollen provided). Each treatment group typically contained five flowers. Hand-pollinations involved brushing freshly dehisced anthers against receptive stigmas to cover them with pollen grains.

In 1999, flowers from treatment group *iii* failed to produce fruits, so I used paired two-tailed t-tests to compare mean fruit set and mean seed set between treatment groups *i* and *ii*. In 2000, I compared mean fruit set among treatment groups *i*, *ii*, and *iii* using two-way ANOVAs (with treatment as the main effect and plant as a block effect) followed by Tukey's HSD Multiple Comparison Tests. I compared mean seed set among the three groups using a nested ANOVA with treatment nested within plant. Four plants in 1999 and 16 plants in 2000 were excluded from the analysis due to either anther smut disease or inability to replicate all three experimental treatments on a single plant.

Determining the Importance of Biotic versus Abiotic Pollination

In 2000, I conducted an experiment to assess the relative contribution to fruit and seed set made by autogamy, insect visitation, and jostling-

TABLE 1. RELEVANT COMPARISONS AND THEIR IMPLICATIONS FOR THE EXPERIMENT DESIGNED TO DETERMINE THE RELATIVE IMPORTANCE OF ABIOTIC VERSUS BIOTIC SOURCES OF POLLEN IN 2000. Pollen sources available to plants included in each treatment group (caged, emasculated, pruned, or unmanipulated) are included in parentheses (a = autogamy, i = insect visitation, and j = jostling-induced geitonogamy). See also caveats described in the Results and Discussion sections.

Implications of Pairwise Treatment Comparisons
— If fruit/seed set of unmanipulated plants (a, i, j) > pruned plants (a, i), then jostling contributes pollen (provided that visitation rates to pruned and unmanipulated plants are similar and pruning does not reduce a plant's attractiveness to pollinators).
— If fruit/seed set of unmanipulated plants (a, i, j) = emasculated plants (i), then insect visitation and/or autogamy contributes pollen and jostling-induced geitonogamy does not contribute pollen.
— If fruit/seed set of pruned plants (a, i) > emasculated plants (i), then autogamy contributes pollen.
— If fruit/seed set of unmanipulated plants (a, i, j) > caged plants (a, j), then insect visitation contributes pollen.

induced geitonogamy. I randomly selected and assigned 160 plants to one of the following four treatment groups: *i.* caged for the duration of its flowering; *ii.* emasculated (removal of all anthers on the plant); *iii.* pruned (selective removal of inflorescences to prevent flowers from contacting others on the same plant or neighboring plants); or *iv.* unmanipulated (all inflorescences and anthers left intact). Each treatment group contained 40 plants. Pruned plants retained three to five inflorescences.

By differing in available sources of pollen, each experimental treatment group provided an insight regarding the importance of different pollination sources to reproduction (Table 1). Yet it should be noted that by imposing these treatments, I potentially introduced the additional sources of variation (also see Discussion section) described below. For example, caging plants provided a measure of maternal reproductive success in the absence of insect visitors. However, cages also sheltered plants from slight breezes and the window-screening mesh may have provided a surface to which sticky inflorescences could adhere; this potentially reduced, but could not eliminate inflorescence jostling within a plant. By emasculating plants, I could evaluate the contribution of insect visitation by itself to fruit and seed production. Pruning inflorescences ruled out jostling-induced geitonogamy, but autogamy and insect visitation remained as potential means of pollination. However, emasculated plants may have been less attractive to pollen-foraging insects and pruned plants (with their reduced floral displays) may have been less attractive to insects in general. The unmanipulated plants provided an overall estimate of maternal reproductive success attributable to all three possible pollination sources.

I compared mean fruit set, as well as mean seed set, among the treatment groups using one-way ANOVAs followed by Fisher's LSD Multiple Comparison Tests. By comparing pairs of treatments differing by just one source of pollen, I could estimate the importance of each pollen source to fruit and seed set (Table 1). For example, I predicted that if jostling contributed pollen, then unmanipulated plants (all three sources of pollen possible) would have higher fruit and seed set than pruned plants (only autogamy and insect-borne sources of pollen possible). I removed 48 plants from the analysis because of either herbivory or anther smut disease (to evaluate the distribution of these removals across treatments, refer to actual sample sizes presented in Table 6).

RESULTS

Identities of Floral Visitors and Visitation Rates

During both years, I recorded a total of at least seven taxa of visiting insects (Table 2). Flies (Diptera) and moths (Lepidoptera) made the majority of visits. Bees (Hymenoptera) also visited the flowers, but were much less common (Table 2). I observed an additional seven visits by small flies that could not be caught for identification.

The identities of insect visitors varied between 1999 and 2000. Even though *S. lemmonii*'s pale petals are most conspicuous at night, I observed no nocturnal visits during six hours of twilight and nocturnal observation in 1999. Instead, pollen-foraging syrphid flies (Syrphidae) visited most often in that year (Table 2). In 2000, on the other hand, nectar-foraging moths (Noctuidae) were the most frequent floral visitors with eight visits recorded over 11 hrs of twilight and nocturnal observation. Diurnal bees and flies also visited plants during the day in 2000. In both years, yellow-headed bumblebees (*Bombus vosnesenskii*) rarely visited (Table 2), but were abundant at the site, commonly foraging on neighboring snowberry (*Symphoriocarpos mollis*) and lupin (*Lupinus latifolius*) flowers.

Insect visitation was infrequent in both 1999 and 2000. I recorded 26 insect visits over 16 hrs

TABLE 2. INSECT VISITORS TO *SILENE LEMMONII* OBSERVED IN 1999 AND 2000 AND THEIR ESTIMATED VISITATION RATES. Visitation rates were calculated based on the average number of open flowers per plant (24.56). Twenty-six plants were observed for 16 hrs (10 daylight hrs, 6 twilight or night hrs) in 1999 and 57 plants were observed for 20 hrs (9 daylight hrs, 11 twilight or night hrs) in 2000. The pooled visitation rate (visitation rate pooled for all insect taxa in a year) was 2.54×10^{-3} visits flower^{-1} hr^{-1} in 1999 and 7.86×10^{-4} visits flower^{-1} hr^{-1} in 2000. Unknown flies were observed visiting, but could not be caught for identification.

Year	Insect Taxon (Order)	Number of Observed Visits	Visitation Rate (# visits flower^{-1} hr^{-1})
1999	*Bombus vosnesenskii* (Hymenoptera)	1	9.8×10^{-5}
	Syrphidae (Diptera)	16	1.6×10^{-3}
	Megachilidae (Hymenoptera)	4	3.9×10^{-4}
	Unknown Fly (Diptera)	5	4.9×10^{-4}
2000	*Bombus vosnesenskii* (Hymenoptera)	1	3.6×10^{-5}
	Noctuidae (Lepidoptera)	8	2.9×10^{-4}
	Syrphidae (Diptera)	6	2.1×10^{-4}
	Megachilidae (Hymenoptera)	3	1.1×10^{-4}
	Osmia sp. (Hymenoptera)	1	3.6×10^{-5}
	Bombyliidae (Diptera)	1	3.6×10^{-5}
	Unknown Fly (Diptera)	2	7.1×10^{-5}

of observation in 1999 and 22 visits over 20 hrs of observation in 2000. Consequently, taxon-specific visitation rates calculated for each visitor taxon were extremely low in both years of the study (Table 2), as were visitation rates pooled across all insect taxa. The visitation rate pooled across all insect taxa was 2.54×10^{-3} visits flower^{-1} hr^{-1} in 1999 and 7.86×10^{-4} visits flower^{-1} hr^{-1} in 2000, based on an estimated average number of 24.56 open flowers per plant. I predicted that an individual flower had little chance of receiving a single visit during its lifetime for both years of this study. Based on the pooled visitation rates estimated for the study population, a single flower could expect to receive 0.55 visit in 1999 and 0.09 visit in 2000.

Both of the sensitivity analyses I conducted indicated that both visitation rate and the expected visit number over the floral lifetime remain low even when I vary the estimates of average number of open flowers and the duration of the floral lifespan (Fig. 2). I examined the impact of varying flower number on calculated visit rates because I was concerned that my estimate of the average number of open flowers per plant may have been too high. However, even when I reduce average the number of open flowers per plant to 10, calculated rates remain very low (6.25×10^{-3} in 1999 and 1.93×10^{-3} in 2000). Additionally, the total number of insect visits over a flower's lifetime is likely an over-estimate because insects were not active for all 120 hrs of a flower's lifetime. For instance, I never observed insect visitors in the early morning (0100–0300), but flowers stayed open during those hours. A flower's probability of receiving a visit decreases if I account for the number of hours insects may be available. If, for example, insects visit flowers for only 100 hr of the floral lifetime, a single flower could expect 0.25 visit in 1999 and 0.08 visit in 2000.

Proportion of Pollination Occurring During Daytime versus Evening Hours

During both field seasons, caging plants for some portion of a 24-hour period decreased fruit production. In 1999, flowers accessible to visitors throughout the day and night produced more fruits than did flowers exposed only during the day (Table 3). Fruit set among night-exposed plants did not statistically differ from that of plants exposed during the day or that of uncaged plants (Table 3). Mean seed set did not differ among the three treatment groups in 1999 (Table 3).

In 2000, uncaged plants exhibited significantly greater fruit set and seed set than those exposed solely during the day or night (Table 3). Unlike the previous year, night-exposed plants in 2000 had greater fruit set and seed set than day-exposed plants (Table 3). Excluding visitors during either the day or night also reduced seed production in 2000. However, night-exposed plants had greater seed set than those exposed during the day (Table 3).

Timing of Male and Female Phases of Floral Development

Silene lemmonii flowers are strongly protandrous with very little overlap of their male and female phases; filaments are extended and anthers shed pollen prior to stigma receptivity. In 1999, the male phase lasted for average of 2.7 d (SE = 0.55) and the female phase lasted for an average of 6.4 d (SE = 0.86). In 2000, the male phase lasted for an average of 2.79 d (SE = 0.15) and

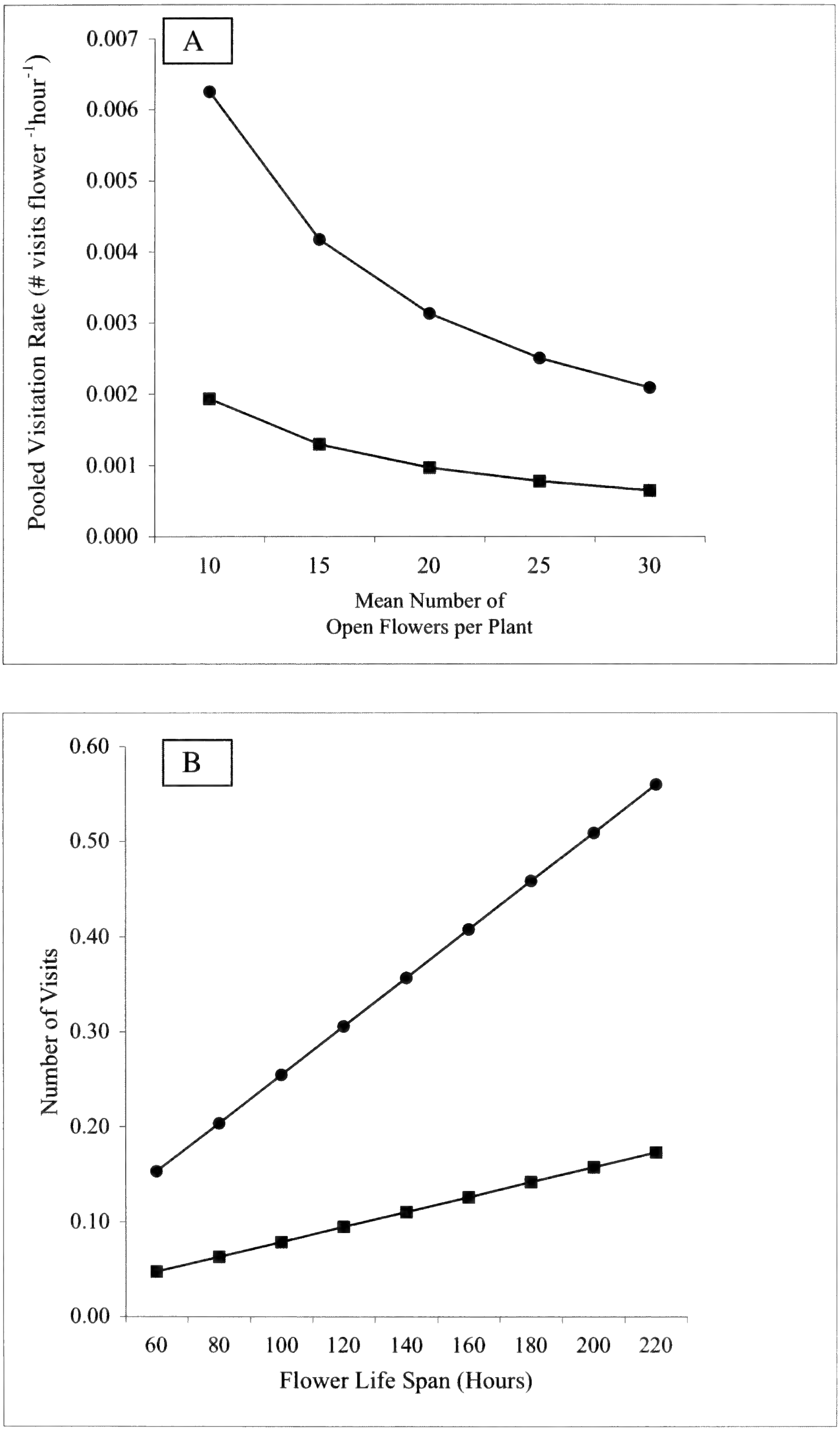

FIG. 2. Results of sensitivity analyses evaluating: A. the effect of varying average flower number on the estimation of the pooled insect visitation rate; and B. the effect of varying flower life span on the estimated number of visits a flower receives over its lifetime. Estimation of visit number is based on the average number of open flowers per plant (24.56). Circles (●) indicate results from 1999; squares (■) indicate results from 2000.

TABLE 3. COMPARISON OF MEAN FRUIT AND SEED SET OF PLANTS THAT WERE UNCAGED, EXPOSED ONLY DURING THE DAY, OR EXPOSED ONLY AT NIGHT IN 1999 AND 2000. For each year means with identical superscripts are not significantly different (Fisher's LSD Multiple Comparison Test, $P < 0.05$). N = the number of plants per treatment. For some treatments, seed set N < fruit set N because Lepidoptera larvae consumed all the seeds produced by a plant. NS = not significant, * = $P < 0.05$, ** = $P < 0.005$.

Year	Treatment	Mean Fruit Set (SE)	N	F-ratio	Mean Seed Set (SE)	N	F-ratio
1999	Day open	0.09 (0.035)^{a}	7	4.51*	6.15 (0.64)^{a}	6	0.69^{NS}
	Night open	0.17 (0.065)^{ab}	7	df = 2, 57	6.88 (1.23)^{a}	5	df = 2, 61
	Day and night open	0.40 (0.049)^{b}	46		6.78 (0.96)^{a}	20	
2000	Day open	0.23 (0.031)^{a}	19	34.57**	6.89 (0.58)^{a}	18	54.43**
	Night open	0.34 (0.037)^{b}	24	df = 2, 70	9.22 (0.43)^{b}	22	df = 2, 606
	Day and night open	0.61 (0.032)^{c}	30		12.71 (0.26)^{c}	30	

the female phase lasted for an average of 2.11 d (SE = 0.16).

Self-compatibility

Silene lemmonii appears to be fully self-compatible. Fruit set and seed set of self-pollinated flowers matched that of outcrossed flowers in both years of the study. In 2000, both treatment groups had greater fruit set than in the previous year (Tables 4 and 5). Additionally, flowers appear to have little capacity for autogamy. In 1999, none of the caged, unmanipulated flowers produced fruits. In 2000, approximately 12% of the caged, unmanipulated flowers produced fruits, but seed set of these fruits was low compared to that of self-pollinated and outcrossed fruits (Tables 4 and 5).

Effects of Pruning, Caging, or Emasculating Flowers on Fruit Set and Seed Set

Mean fruit set differed among the four experimental treatment groups (one-way ANOVA, $F_{3,108} = 35.02$, $P < 0.001$; Table 6). On average, approximately 61% of flowers on unmanipulated plants set fruit, exhibiting greater fruit set than plants from the other three treatment groups (Table 6). In contrast, caged plants set significantly fewer fruits (~10%) than the other three groups. Fruit set experienced by pruned plants (~46%) did not differ statistically from that of emasculated plants (~49%) (Table 6).

Seed set varied among the four treatment groups (Table 6). However, the differences in seed set among the groups did not directly correspond with the differences found in fruit set, and average seed set differed statistically among all four treatment groups. Pruned plants had the greatest seed set, followed by unmanipulated plants, emasculated plants, and then caged plants (one-way ANOVA, $F_{3,\ 726} = 65.83$, $P < 0.0001$; Table 6).

DISCUSSION

For many years, the level of specialization versus generalization characterizing plant-pollinator interactions has been the subject of robust debate (Waser et al. 1996; Johnson and Steiner 2000; Gómez 2002). Pollination syndromes, or the presence of highly specific suites of floral traits that attract particular pollinators or facilitate a specialized type of pollination (Procter et al. 1996), are an intuitive and appealing way to both explain the large diversity of both flowering plants and pollinating animals and to gain a preliminary understanding of plant-animal coevolutionary processes. However, numerous studies indicate that flowering plants receive pollination services from many different animal

TABLE 4. COMPARISON OF MEAN FRUIT AND SEED SET BY SELF-POLLINATED, OUTCROSSED, AND UNMANIPULATED CAGED FLOWERS IN 1999 AND 2000. For each year means with the same superscripts are not significantly different (Paired t-test or Tukey's HSD Multiple Comparison Test, $P < 0.05$). N = the number of plants per treatment. NS = not significant, * = $P < 0.05$, ** = $P < 0.005$, *** = $P < 0.0005$.

Year	Treatment	Mean Fruit Set (SE)	N	Test statistic	Mean Seed Set (SE)	N	Test statistic
1999	Self-pollinated	0.42 (0.11)^{a}	16	t = 0.58^{NS}	5.41 (1.29)^{a}	8	t = 0.78^{NS}
	Outcrossed	0.33 (0.096)^{a}	16		7.00 (1.60)^{a}	9	
	Unmanipulated	0	16		—	—	
2000	Self-pollinated	0.55 (0.063)^{a}	24	F = 4.75***	10.93 (0.94)^{a}	24	F-ratio = 2.55***
	Outcrossed	0.61 (0.065)^{a}	24		12.65 (0.84)^{a}	24	
	Unmanipulated	0.12 (0.052)^{b}	24		4.40 (1.97)^{b}	24	

TABLE 5. THE EFFECTS OF POLLINATION TREATMENT (SELF, OUTCROSS, AND CONTROL) AND MATERNAL PLANT ON FRUIT SET AND SEED SET IN 2000. Fruit set was compared with a two-way ANOVA, with plant as a block effect. Seed set was compared using a nested ANOVA, with treatment nested within plant.

	df	SS	F-ratio	P
Fruit Set				
Model	25	6.79	4.75	<0.0001
Plant	23	3.34	2.53	0.0036
Treatment	2	3.45	30.17	<0.0001
Error	46	2.63		
Seed Set				
Model	50	3221.18	2.55	0.0003
Treatment	2	533.52	10.57	0.0001
Treatment (plant)	48	2639.3	2.18	0.0024
Error	58	4685.56		

taxa (Stephenson and Thomas 1977; Herrera 2005; Buide 2006). Furthermore, pollinator abundances can vary over space and time (Moeller 2005; Price et al. 2005). This spatiotemporal variation in pollination service is one factor thought to promote self-fertilization in plant species (Kalisz and Vogler 2003; Morgan and Wilson 2005). In populations with low inbreeding depression, selfing can provide reproductive assurance when pollinators are scarce (Eckert and Schaefer 1998; Fausto et al. 2001).

The main goal of this study was to study *S. lemmonii*'s pollination biology, which was relatively unknown previously. Invoking the concept of pollination syndromes, one would expect a night-blooming plant with pale petals such as *S. lemmonii* to be moth-pollinated (Proctor et al. 1996). Although *S. lemmonii* attracts noctuid moths during twilight and night hours, bees and flies visit flowers during daylight hours. Thus, a mixed pollination system (with both diurnal and nocturnal animals contributing to fruit set) appears to operate in the study population. Previous studies have also documented diurnal and nocturnal pollination of night-blooming plants (Barthnell and Knops 1997; Young 2002; Barthelmess et al. 2006; Dar et al. 2006; Saunders and Sipes 2006). In both years of this study, plants allowed access to daytime and evening pollination produced the most fruits and seeds. An overall increase in fruit and seed set in 2000, the only year when I recorded noctuid moth visitation, suggests that these moths may be very efficient pollinators and that pollen limitation may occur in years when moths are absent. The fact that night-exposed plants exhibited greater fruit and seed set than their day-exposed counterparts in 2000 supports these hypotheses.

Visitor identity varied between years at the study site; this could be due in part to two factors. First, *S. lemmonii* flowers provide almost no nectar for pollinators (A. Hove, unpublished data). Therefore, nectar-foraging moths had little incentive to visit regularly and moth populations may not be well established at the site. Second, slight interannual differences in abiotic environmental parameters (such as temperature, soil moisture, or relative humidity) may help explain both differences in visitation rates between years and the absence of moths in 1999. While I did not regularly measure environmental variables, I also did not observe any dramatic differences in climate or the onset of flowering between the 1999 and 2000 flowering seasons. Additionally, in both years, I regularly observed insects foraging on other flowering plant species at the site.

Regardless of the differences in visitor identity observed between 1999 and 2000, diurnal and nocturnal insects only rarely visited flowers during those years. In 1999, the estimated visit

TABLE 6. COMPARISON OF MEAN FRUIT SET AND SEED SET OF PLANTS THAT WERE CAGED, PRUNED, EMASCULATED, OR UNMANIPULATED IN 2000. Pollen sources for each treatment are included in parentheses (a = autogamy, i = insect visitation, and j = jostling-induced geitonogamy). Means from the same year with different superscripts are significantly different (Fisher's LSD Multiple Comparison Test, $P < 0.05$). N = number of plants per treatment.

Treatment	Mean Fruit Set (SE)	N	Mean Seed Set (SE)	N
Caged (a, j)	0.10 (0.014)^{a}	29	4.47 (0.57)^{a}	20
Emasculated (i)	0.49 (0.039)^{b}	31	10.36 (0.33)^{b}	31
Pruned (a, i)	0.46 (0.064)^{b}	22	14.82 (0.86)^{c}	17
Unmanipulated (a, i, j)	0.61 (0.032)^{c}	30	12.71 (0.24)^{d}	30

number over a flower's lifetime (0.55 visits/flower) roughly corresponded to the average fruit set of open-pollinated plants (~40%). The estimated total of 0.55 insect visits per flower suggests that approximately one out of two flowers in the study population received a visit.

The low pooled visitation rate observed in 2000, which corresponds to an estimated 0.09 visit per flower over its lifetime, is more difficult to reconcile with that year's relatively high fruit set (~61%). One possible explanation for the discrepancy between fruit set and the pooled insect visitation rate is that insect visits occurred more frequently than observed, particularly at night when pairs of field workers used red lights to illuminate the plants. Although red lights have been used to observe visits to other *Silene* species (Pettersson 1991) as well as other moth-pollinated species (see Kearns and Inouye 1993), it is conceivable red lights may have repelled nocturnal visitors to *S. lemmonii*, leading to low calculated visitation rates for nocturnal insects.

Despite low insect visitation rates, fruit production at the study site appears to have been primarily insect-mediated in 2000. Almost half of the emasculated flowers set fruit, whereas ~61% of unmanipulated plants set fruit. The difference in fruit set between emasculated flowers (allowed only insect visits as a pollen source) and unmanipulated flowers suggests that insect pollination accounted for ~80% of fruit production of unmanipulated plants (Fig. 3). Other evidence suggests that the remaining 20% resulted from jostling-induced geitonogamy. Pruned plants had lower fruit set than unmanipulated plants (Table 6), indicating that jostling-induced geitonogamy aided in fruit production and/or that pruning inflorescences reduced insect visitation. Furthermore, fruit set of emasculated plants was about 12% lower than that of unmanipulated plants (Table 6), implying that jostling-induced geitonogamy contributed to the remaining ~20% of fruit production (Fig. 3).

Comparison of fruit set between the pruned and emasculated groups suggests that autonomous self-fertilization by autogamy did not occur. Flowers exposed to insect pollination and autogamy as potential pollen sources were as likely to set fruit as those solely dependent on insect visitors. Fruit set of caged plants was significantly less than fruit set in the other groups (Table 6), underscoring insect visitation as the most important component of pollination. Still, ~10% of the caged flowers developed into fruits, the result of either jostling-induced geitonogamy or autogamy. However, since flowers are strongly protandrous, I suspect that autogamy contributed minimally (if at all) to fruit set; fruit production by caged plants more likely resulted from jostling-induced geitonogamy.

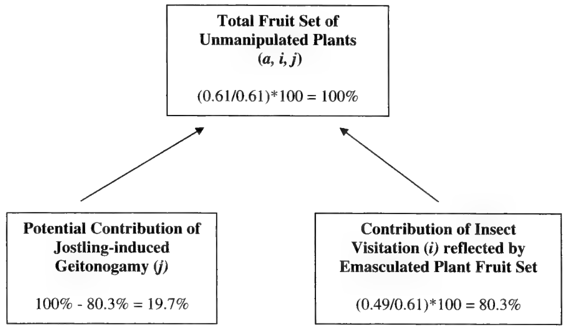

FIG. 3. Flowchart depicting the relative contribution of each source of pollen to total fruit set. If insect visitation (*i*) contributes ~80% and the probability of autogamy (*a*) is low, then jostling-induced geitonogamy (*j*) potentially contributes to ~20% of fruit set.

The results of this study provide evidence that jostling-induced geitonogamy contributes to fruit production in *S. lemmonii*. However, before fully accepting jostling-induced geitonogamy as a pollen transfer mechanism, three potential weaknesses in my experimental design must be addressed.

First, pruned plants may have been less attractive to foraging insects than unmanipulated plants. Reduced fruit set of pruned plants may have in turn resulted from fewer insect visits, rather than inflorescences' inability to jostle into one another. (Nonetheless, pruning plants was the most practical and feasible way to restrict jostling among inflorescences.) While some studies on other plant species have found that fruit set is not influenced by local plant density (Pettersson 1997; Bosch and Waser 1999; Somanathan et al. 2004), other studies (Brys et al. 2004; Somanathan et al. 2004) have clearly shown reduced fruit set in low-density plant populations. However, if pruned plants received fewer visits from insects attracted to large floral displays, then one would expect plants occurring in denser patches and displaying many flowers to have higher fruit set. A preliminary experiment I conducted in 1999 showed that neither local plant density nor the number of flowers per plant affected fruit and seed set in my study population. Though the density and pruning studies were not conducted simultaneously, the data imply that pruning plants had a minimal impact on their ability to attract insects.

Second, reduced fruit production by pruned plants is potentially attributable to two factors: the inability of flowers to jostle into one another and the injury inflicted upon plants by pruning inflorescences. I attempted to minimize plant injury by only clipping inflorescence rachises and leaving foliage leaves and vegetative stems untouched. However, future research on jostling-induced geitonogamy in *S. lemmonii* would benefit from developing a method to spatially

separate inflorescences without pruning them. Interestingly pruned plants produced more seeds than plants from the other three treatment groups (Table 6), possibly because with fewer flowers pruned plants could allocate more resources to each fruit for seed production. Other studies have also shown increases in reproductive output following the partial loss of plant parts (Mabry and Wayne 1997; Fang et al. 2006).

Third, lower fruit set of emasculated plants in comparison to unmanipulated ones could be attributed to fewer visits by pollen-foraging insects. However, these plants were, with the exception of bare stamens, similar in floral display to unmanipulated ones. Moreover, syrphid flies, presumably foraging on pollen, landed on female-phase flowers, even when withered stamens displayed no fresh pollen (A. Hove, *personal observation*).

Although insect pollination and jostling-induced geitonogamy evidently contributed to fruit set in 2000, the possibility of wind pollination should also be considered. Goodwillie's (1999) study of *Linanthus parviflorus* showed that wind pollination provides reproductive assurance when insect visitation is low. However, her study site was a relatively open area, consisting of oak woodlands and grasslands. Wind pollination of other entomophilous species growing in windy, exposed areas has also been recorded (Gómez and Zamora 1996; Norman et al. 1997; Lazaro and Traveset 2005). Because the forest understory surrounding Dubakella Mountain is sheltered from wind, long-distance travel by pollen grains on wind currents does not seem likely. However, a future study involving the placement of pollen traps next to flowers throughout the population using methods similar to Goodwillie's (1999) is necessary to rule out the possibility of wind pollination in *S. lemmonii*.

Although no previous studies have documented it, jostling-induced geitonogamy probably occurs in other self-compatible plant species. This type of self-pollination seems especially likely to operate in plant species that produce several inflorescences bearing pendant flowers with exerted reproductive structures. Jostling-induced geitonogamy may also serve as an additional pollination source for species where autogamy is unlikely to occur because flowers separate pollen presentation from stigma receptivity either spatially (herkogamy) or temporally (dichogamy).

In summary, the majority of fruit production resulted from diurnal and nocturnal insect pollination in my study population, yet jostling-induced geitonogamy likely contributed to fruit set. Recent work has shown that mixed mating systems, wherein individuals reproduce via a combination of selfing and outcrossing, may be more common than previously thought (Goodwillie et al. 2005); besides *S. lemmonii*, mixed mating also occurs in multiple *Silene* species (Kephart et al. 1999; Davis and Delph 2005; Keller and Schwaegerle 2006). However, at the study site *S. lemmonii* appears to self-pollinate by jostling-induced geitonogamy rather than autogamy. Yet, it seems unlikely that jostling-induced geitonogamy has evolved as a mechanism to promote reproductive assurance in *S. lemmonii*. A more likely explanation lies in the fact that the glandular inflorescence trichomes that facilitate floral jostling serve primarily to protect plants from crawling herbivores. Trichomes are a well-known herbivore defense mechanism (Hare and Elle 2004; Handley et al. 2005). Instead of a mating system adaptation, selfing via floral jostling may be an incidental process that can persist in populations where inbreeding depression is low enough for the defensive benefits of glandular inflorescence trichomes to outweigh any costs associated with selfing. However further empirical work examining the potential role of herbivory in the maintenance of mixed mating in multiple *S. lemmonii* populations is needed to confirm this hypothesis.

In the population I studied, inbreeding depression does not appear to limit self-fertilization. Self-pollinated flowers produced seeds and fruits as well as outcrossed ones during the years of this study. However, to fully understand the potential effect of inbreeding, future studies should examine the genetic structure of *S. lemmonii* populations and compare selfing rates as well as fitness among populations from various locations in this species' geographic range. Comparing the progeny of selfing and outcrossing plants using other measures of fitness, such as seedling survival and seedling vigor, will also provide greater insights regarding the implications of mixed mating in this species.

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PEDICULARIS AURANTIACA AND *PEDICULARIS DENSIFLORA* (OROBANCHACEAE): TAXONOMY, PHENOLOGY AND FLORAL MORPHOLOGICAL VARIATION

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ABSTRACT

We investigated patterns of infraspecific variation among populations of *Pedicularis densiflora*, including populations formerly recognized as *P. densiflora* subsp. *aurantiaca*. Several statistical analyses (UPGMA, ANOVA, and PCA) were conducted on floral traits measured in the field. All three statistical analyses indicated consistent differences in floral morphology among populations. These differences were confirmed by a review of over 1000 herbarium specimens. Two series of populations were separated, and two species recognized, **Pedicularis aurantiaca** and *P. densiflora*. *Pedicularis aurantiaca* had large calyces with floral tubes included at anthesis, reduced lower labia, and enlarged galea openings. *Pedicularis densiflora* had short calyces with fully exserted floral tubes, enlarged lower labia, and smaller galea openings. Taxonomy, phenology, and floral differences are discussed in the context of previously published data on pollinator visitation.

Key Words: California Flora, Morphological Variation, Oregon Flora, Orobanchaceae, *Pedicularis aurantiaca*, *Pedicularis densiflora*.

Pedicularis L. (Orobanchaceae, formerly Scrophulariaceae) is a large (approximately 500 species), monophyletic genus of hemiparasitic herbs, with a northern temperate distribution and tremendous diversity in floral morphology (Ree 2005). The genus has undergone a relatively recent diversification, likely in the Pleistocene, and shares a center of diversity in eastern Asia with its primary pollinator, *Bombus* (De-Yaun 1983). Considerable research has investigated the reproductive biology of *Pedicularis* and documented the modes of plant-pollinator interaction (e.g., Sprague 1962; Grant 1966; Grant and Grant 1967; Macior 1973, 1977, 1982, 1983, 1984, 1986a, b, 1995a, b, 1996, 1997 and references therein; Wang 1998a, b; Robart 2005).

Pedicularis densiflora Benth. ex Hook., a species found only in California and southern Oregon, was first described from a communication with Douglas by Bentham, and published by J. W. Hooker (1838). Sprague (1958) proposed dividing the taxon into two subspecies, *P. densiflora* subsp. *densiflora* and *P. densiflora* subsp. *aurantiaca* E. F. Sprague. Her subspecific circumscriptions were based on distribution, reproductive biology, phenology, host affinity, and floral morphology (Sprague 1958, 1960, 1961, 1962).

According to Sprague (1958), *P. densiflora* subsp. *densiflora* is pollinated by both *Bombus* and hummingbirds while *P. densiflora* subsp. *aurantiaca* is pollinated exclusively by hummingbirds. Macior (1986a) documented pollinator type, frequency, and mode of pollination of both subspecies. Macior's (1986a) research supported Sprague's (1958, 1962) conclusion that the subspecies have different pollination systems. Sprague (1962) and Macior (1986a) suggested that hummingbird pollination was driving a change in morphology among populations and creating a shift from a bumblebee pollination syndrome to a hummingbird syndrome.

There have been no detailed quantitative morphological studies to document the morphological divergence among the populations. There has been no attempt to relate morphological variation to the different pollinator systems in the two subspecies. An extensive examination was undertaken to detect and explain patterns of infraspecific variation among populations of the two subspecies.

MATERIALS AND METHODS

Herbarium Specimens

A total of 1069 herbarium specimens of *Pedicularis densiflora* subsp. *densiflora*, *P. densiflora* subsp. *aurantiaca*, and *P. semibarbata* A. Gray from CAS, DS, JEPS, K, MSC, ORE, OSC, POM, RSA, UC, and WILLU were studied. Specimens were examined to locate population study sites and identify morphological characters for measurement. Additional retrospective analyses of herbarium specimens were

TABLE 1. LIST OF POPULATIONS AND VOUCHER SPECIMENS FOR FLORAL MORPHOLOGICAL ANALYSIS OF *PEDICULARIS DENSIFLORA* SUBSP. *DENSIFLORA* AND *P. DENSIFLORA* SUBSP. *AURANTIACA*. All voucher specimens are deposited at Michigan State University Herbarium (MSC)

Species	Location (County, State)	Voucher
P. aurantiaca	Inskip (Butte Co., CA) N 39°59.541′, W 121°32.389′, 1309 m	Monfils 37
P. aurantiaca	McBride Springs (Siskyou Co., CA) N 41°20.687′, W 122°16.506′, 1500 m	Monfils 43
P. aurantiaca	Pinehurst (Jackson Co., OR) N 42°07.452′, W 122°20.783′, 1167 m	Monfils 40
P. densiflora	Bear Valley (Colusa/Lake Co., CA) N 39°09.504′, W 122°28.778′, 810 m	Monfils 33
P. densiflora	Hurles Circle (Butte Co., CA) N 39°29.764′, W 121°22.632′, 625 m	Monfils 35
P. densiflora	Missouri Flats Road (Josephine Co., OR) N 42°19.288′, W 123°13.871′, 1188 m	Monfils 36
P. densiflora	Mount Diablo (Contra Costa Co., CA) N 37°51.814, W 121°55.770′, 777 m	Monfils 28
P. densiflora	Paradise (Marin Co., CA) N 37°53.329′, W 122°26.954′, 33 m	Monfils 34
P. densiflora	Round Valley Historical Marker (Mendocino Co., CA) N 39°43.749′, W 123°15.112′, 658 m	Monfils 32
P. densiflora	Santa Margarita Lake (San Luis Obispo Co., CA) N 35°17.214, W 120°28.659′, 670 m	Monfils 21

conducted to evaluate utility and reliability of the morphological traits used to distinguish the two subspecies, and to comprehensively review the distribution of the two taxa. Each specimen was examined and key diagnostic features were assessed to determine subspecies identification. After herbarium specimens were examined and identified, distribution, elevational range, and phenological data were gathered.

Analysis of Floral Morphological Variation

Study populations were selected from throughout the range of *Pedicularis densiflora* subsp. *densiflora* and *P. densiflora* subsp. *aurantiaca*, sampling a broad elevational (30 to 1500 m) and geographic spectrum. Populations were chosen to represent the full breadth of morphological diversity previously described within *P. densiflora* (Sprague 1958, 1960, 1961, 1962). During a preliminary field season in 1998, sixteen localities were screened and ten populations were chosen for the study of floral morphological divergence. Populations were selected prior to measurement or subspecific determination. Population choice was based on population size and feasibility of using the site. Several populations located in the southern part of the range were peripheral populations consisting of few (3+) or scattered plants and could not be used to represent morphological variability. The Auberry Road population in the Southern Sierra Nevada Mountains was inaccessible for study after the initial field season due to weather and road conditions. Plants from these southern populations were vouchered and collections were retroactively studied. Populations used in the morphological study were from the following ten localities: Bear Valley (Colusa/Lake Co., CA), Hurles Circle (Butte Co., CA), Inskip (Butte Co., CA), McBride Springs (Siskyou Co., CA), Missouri Flats Road (Josephine Co., OR), Mount Diablo (Contra Costa Co., CA), Paradise (Marin Co., CA), Pinehurst (Jackson Co., OR), Round Valley Historical Marker (Mendocino Co., CA), and Santa Margarita Lake (San Luis Obispo Co., CA). Voucher specimens were deposited in the Michigan State University Herbarium (MSC; Table 1, Fig. 1A and B).

When available, 50 individuals per population were studied. A total of 466 flowers were measured. Within each population, one flower each was removed from each of 50 plants. Plants were selected by sampling at set intervals along transects encompassing the population. Intervals were selected to systematically study plants throughout the population. Floral measurements were made on the most apical flowers that were intact, fully developed, with an exserted stigma, and shedding pollen.

Measurements were made using digital calipers and recorded to the nearest 0.01 mm. Floral characters were selected based on the characters used by Sprague (1958) to differentiate the subspecies, determined by Macior (1986a) to be involved in effective pollination, and suggested by Faegri and Van der Pijl (1966) to be associated with *Bombus* and hummingbird pollination syndromes. Thirteen quantitative characters were measured and/or calculated: galea width (measured as width of laterally compressed galea), tube width (measured as width of laterally

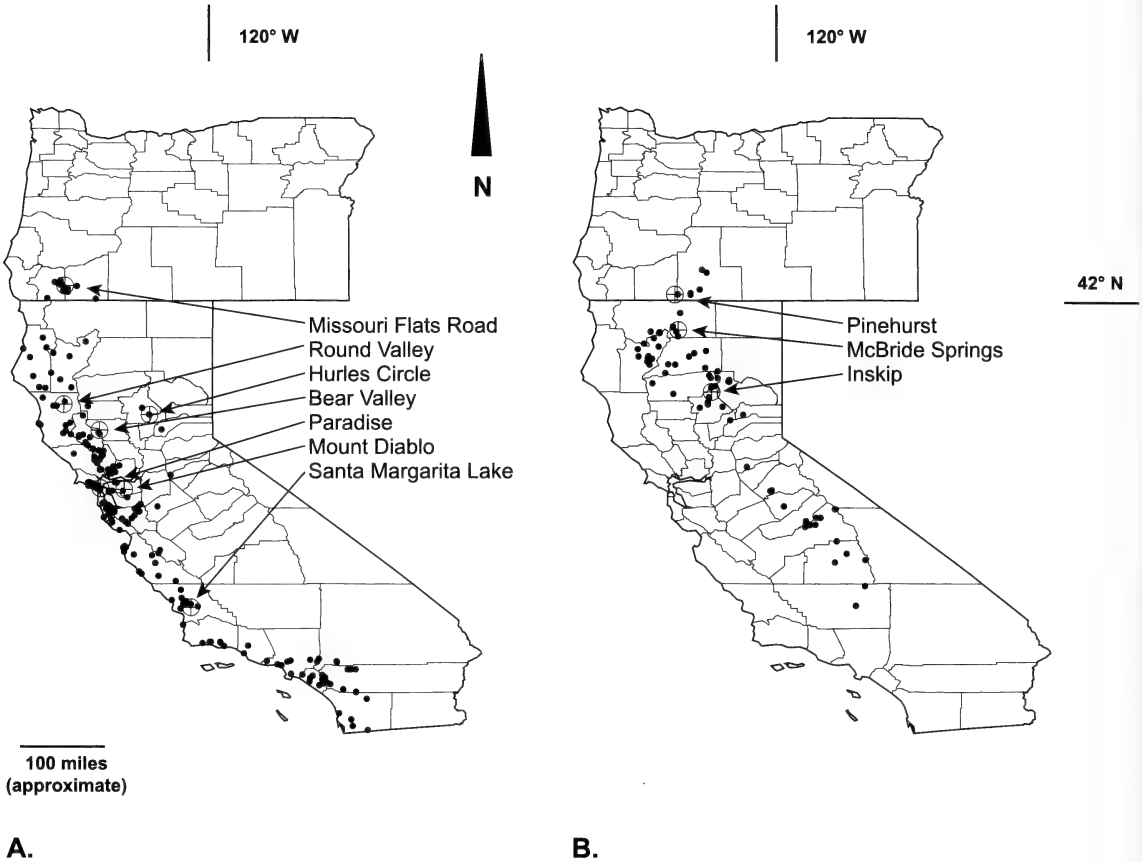

FIG. 1. A. Distribution of population study sites and herbarium specimens of *Pedicularis densiflora* subsp. *densiflora* (Baja California, Mexico site not shown). B. Distribution of population study sites and herbarium specimens of *Pedicularis densiflora* subsp. *aurantiaca*. Herbarium specimen localities determined when possible by GEOLocate (Tulane University Museum of Natural History, Belle Chase, LA). Dot indicates locality and may represent multiple specimens.

compressed tube), galea length, tube length, orifice width (measured as abaxial margin of galea), calyx length, pistil length, stamen length, labium length, axis angle (calculated from the galea length, tube length and length from galea tip to tube/receptacle junction), tube exsertion (calculated by subtracting tube length from calyx length), corolla length (calculated by adding tube and galea length), and labium tip to galea bend length (Fig. 2). Four additional characters were ratios derived from the initial measurements and used to quantify the relationship between shape and size: orifice width/galea length, labium length/galea length, tube length/galea length, and tube width/galea width.

Statistical Analysis

The JMP statistical package (SAS Institute Inc., Cary, NC) was used to perform a non-hierarchical analysis among population means for all 13 quantitative floral morphological characters using principal component analysis (PCA). Ratios derived from initial measurements were not included in the multivariate analysis to avoid spurious correlations (Atchley et al. 1976; Frampton and Ward 1998; Brett 2004). All measurements were standardized across the populations with a mean of zero and a variance of one. Varimax factor rotation (Kaiser 1958) was conducted using 13 rotated factors (Johnson and Wichern 2002).

A dissimilarity matrix was created from the 13 standardized quantitative floral morphological character traits with the program NTSYSpc version 2.1 (Applied Biostatistics, Inc. Setauket, NY) using the average "taxonomic" distance coefficient. The unweighted pair-group method of cluster analysis (UPGMA) was performed on the dissimilarity matrix, and a UPGMA phenogram was constructed.

Analysis of variance (ANOVA) was performed on all 17 characters for the ten populations using the SAS V8 (SAS Institute Inc., Cary, NC). The

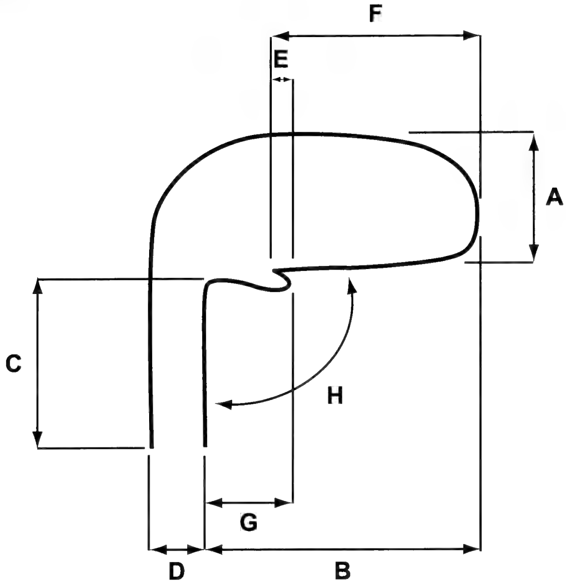

FIG. 2. Schematic representation of *Pedicularis densiflora* corolla. Lines represent parameters of quantitative measurements and letters correspond to the following measurements: A. galea width, B. galea length, C. tube length, D. tube width, E. labium length, F. orifice width, G. labium tip to galea bend length, and H. axis angle.

PROC UNIVARIATE and HOVTEST=LEVENE tests were conducted to test normality and homogeneity of variance, respectively. Where necessary, data were log, square root, or arccosine transformed to better fulfill the assumptions of standard variance and normality. Bonferroni (Dunn) t-tests were conducted on each variable to examine differences between all possible pairs of means and significant groupings among means for all ten populations.

RESULTS

Based on the PCA analysis, greater than 94% of the variance in the data set was explained by the first three factors. Factor one explained 46% of the variation and was weighted at 0.85 or higher for galea width, tube width, orifice width, calyx length, tube exsertion, and labium tip to galea bend length. All these features corresponded to floral shape. Factor two explained 39% of the variation and was weighted at 0.85 or higher for tube length, pistil length, stamen length, and corolla length. These floral characteristics were predominantly attributed to flower size. Factor three explained 9% of the variation in the data set and was not weighted at 0.85 or higher for any of the 13 variables (Table 2).

In the factor by factor analysis of the varimax rotated principal components for the first three factors, factor one clearly separated two distinct clusters of populations: one group consisting of *P. densiflora* subsp. *aurantiaca* populations and a second cluster of *P. densiflora* subsp. *densiflora* populations (Fig. 3). Factors two and three produced a continuum of values which did not separate the populations into any discernable clusters.

The UPGMA phenogram summarized phenotypic similarities among populations. Separation of the populations into two distinct groups was substantiated by the phenogram, which showed high similarity among the *P. densiflora* subsp. *aurantiaca*. populations. The seven populations of *P. densiflora* subsp. *densiflora* were also more similar to each other than they were to the populations of *P. densiflora* subsp. *aurantiaca* (Fig. 4).

All seventeen floral morphological variables (ratios included) showed significant differences among population means ($P < 0.05$) in the ANOVA. Examination of population means

TABLE 2. VARIMAX ROTATED FACTOR PATTERNS OF 13 FLORAL MORPHOLOGICAL TRAITS FOR PCA FACTORS 1–3 OF TEN POPULATIONS OF *PEDICULARIS DENSIFLORA* SUBSP. *DENSIFLORA* AND *P. DENSIFLORA* SUBSP. *AURANTIACA*. The first row shows proportion of variance explained by the first three factors. Varimax rotated factor patterns for the first three factors are listed next to the floral morphological traits.

	Factor 1	Factor 2	Factor 3
Proportion of variance explained by factor	46%	39%	9%
Rotated factor pattern for varimax rotation method			
Galea width	0.936551	0.314562	0.019986
Tube width	0.873642	0.463500	0.09779
Galea length	0.512363	0.710828	0.191500
Tube length	−0.068533	0.917692	0.284838
Orifice width	0.852061	0.425776	−0.217437
Calyx length	0.889926	0.152248	0.123741
Pistil length	0.062068	0.965496	−0.186622
Stamen length	0.201367	0.963109	0.088532
Labium length	−0.814386	0.281443	0.409147
Axis angle	−0.378592	0.542948	0.687267
Tube exsertion	−0.924260	0.301912	0.217005
Corolla length	0.158965	0.939896	0.289686
Labium tip to galea bend length	−0.900535	−0.071308	0.405407

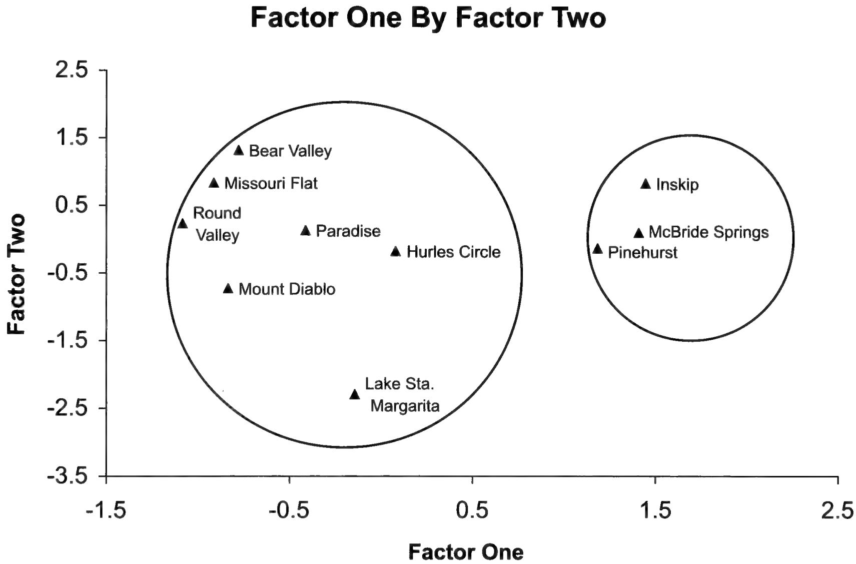

FIG. 3. Plot of factor one by factor two from the varimax rotated principal component analysis of 13 floral morphological characters in ten populations of *P. densiflora* subsp. *densiflora* and *P. densiflora* subsp. *aurantiaca*. Large ellipse represents populations of *P. densiflora* subsp. *densiflora*; small ellipse represents populations of *P. densiflora* subsp. *aurantiaca*.

using the Bonferroni (Dunn) t-tests indicated the *P. densiflora* subsp. *aurantiaca* populations had means not significantly different from each other, but distinct from all populations of *P. densiflora* subsp. *densiflora* for five variables: galea width, orifice width, labium length, orifice width/galea length, and labium length/galea length. Two additional variables (calyx length and labium tip to galea bend) were found to be significantly different between *P. densiflora* subsp. *aurantiaca* and *P. densiflora* subsp. *densiflora*, but the Bonferroni (Dunn) t-tests found statistically different means among *P. densiflora* subsp. *aurantiaca* populations. An examination of the means, and minimum and maximum measurements showed these two characters could also be used to differentiated the populations of *Pedicularis densiflora* subsp. *densiflora* and *P. densiflora* subsp. *aurantiaca*. *Pedicularis densiflora* subsp. *aurantiaca* populations had large mean calyx lengths ($\geq$17 mm) which were larger and significantly different from the *P. densiflora* subsp. *densiflora* populations (all $\leq$14 mm). In the case of mean labia tip to galea bend length, the *P. densiflora* subsp. *aurantiaca* populations had the lowest mean values ($\leq$6 mm) which were significantly different from the *Pedicularis densiflora* subsp. *densiflora* populations with mean measurements $\geq$10 mm (Table 3).

Herbarium specimens and field observations provided data on phenology, elevational range and distribution of the two subspecies. *Pedicularis densiflora* subsp. *aurantiaca* flowers from late April through June and grows at elevations between 600 and 2100 m, with one exception growing at 150 m. *Pedicularis densiflora* subsp. *aurantiaca* is distributed in southeast Oregon in Klamath and Jackson Counties, northern California in the Trinity and Siskiyou Alps, the western slopes of the Sierra Nevada, and as far south as Kern County (Fig. 1B). *Pedicularis densiflora* subsp. *densiflora* flowers from February through April and grows at elevations ranging from 30–1200 m. *Pedicularis densiflora* subsp. *densiflora* is distributed along the coast from southern Oregon to southern California with occurrences as far south as northern Baja California, Mexico. Populations occur in the foothills of the Sierra Nevadas in Butte, Calavaras, and Nevada counties (Fig. 1A). Both subspecies occur in Jackson County in Oregon, and Butte and Trinity Counties in California. Based on field observations and herbarium records the two species do not overlap in population localities, altitude, or flowering time in the three counties where they co-occur (Fig. 1A and B).

Discussion

Herbarium specimens and field collections revealed two series of populations that are morphologically distinct from each other, and correspond to the circumscriptions of the two subspecies *P. densiflora* subsp. *aurantiaca* and *P. densiflora* subsp. *densiflora*. Populations within each series are morphologically cohesive. Based on geographic distribution, altitude and flowering time, *Pedicularis densiflora* subsp. *aurantiaca* is prezygotically isolated from *P. densiflora*

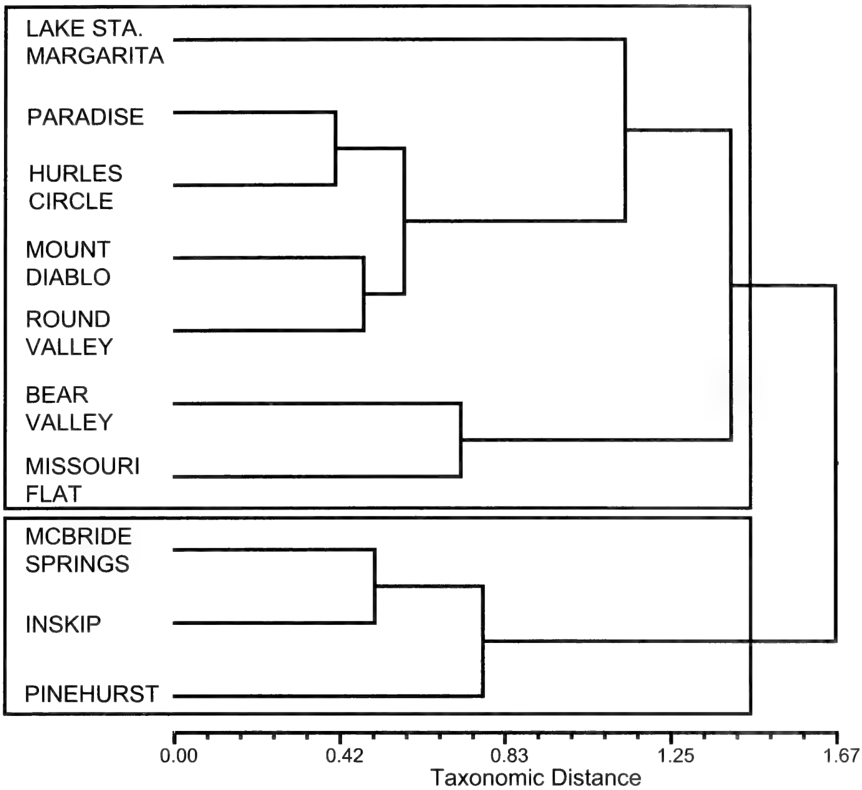

FIG. 4. UPGMA phenogram of taxonomic distance based on 13 continuous floral morphological character traits in populations of *P. densiflora* subsp. *densiflora* and *P. densiflora* subsp. *aurantiaca*. Population names, locations, and voucher information are described in Table 1. Large rectangle represents populations of *P. densiflora* subsp. *densiflora*; small rectangle represents populations of *P. densiflora* subsp. *aurantiaca*.

subsp. *densiflora*. *Pedicularis densiflora* subsp. *aurantiaca* was morphologically distinct, had a later growing season, and typically grew at higher elevations than *P. densiflora* subsp. *densiflora*. Where the two subspecies co-occur in Jackson County in Oregon, and Butte and Trinity Counties in California, *P. densiflora* subsp. *aurantiaca* flowers later than *P. densiflora* subsp. *densiflora* and at higher elevations. Morphological and ecological character traits are sufficiently different to merit species status and *P. densiflora* should be more narrowly circumscribed and *P. densiflora* subsp. *aurantiaca* should be elevated to species status

The new combination is made below, and brief descriptions of the characters that may be used in differentiating the species *Pedicularis densiflora* and *Pedicularis aurantiaca* along with a key are provided.

Pedicularis aurantiaca (E. F. Sprague) Monfils & Prather, comb. et stat. nov. *Pedicularis densiflora* subsp. *aurantiaca* E. F. Sprague, Aliso, 4:130. 1962. Type: USA: from a burn in manzanita brush, Yellow Pine Forest, between the campground and the forest, Lake Almanor, Plumas County, California, at 4300 ft, 30 May 1957, *E. F. Sprague 1202* (holotype: RSA; Isotype RSA!)

Description: Calyx tube 12–24 mm long. Corolla 23–43 mm, deep red to purple to orange-yellow, galea 14–26 mm long, 4–8 mm deep, orifice width 13–23 mm long, lower labium lobes 3–7 mm long from bend in corolla to petal tips. Corolla tube not exserted at anthesis.

600–2100 m. Flowers April through June.

Additional Material seen in Appendix I

Pedicularis densiflora Benth. ex. Hook. Fl. Bor. Am. ii. 110. 1838. Type: Douglas s.n. 1833 (K—4 specimens; photos MSC!).

Synonym: *P. attenuata* Benth. Prodr. (DC.) x. 574. 1846. Isotype: Coulter s.n. (NY, On-line photo!)

Description: Calyx tube 10–18 mm long. Corolla 23–43 mm, deep red to purple to orange-yellow, sometimes white, galea 15–25 mm long, 4–7 mm deep, orifice width 9–20 mm long, lower labium lobes 8–16 mm long from bend in corolla to petal tips. Corolla tube exserted at anthesis.

30–1200 m. Flowers February through April.

Additional Material seen in Appendix II

TABLE 3. SAMPLE SIZE, MEANS, STANDARD DEVIATIONS, MINIMA, MAXIMA AND RESULTS FROM ANOVA AND BONFERRONI (DUNN) T-TESTS FOR CHARACTERS STUDIED IN THE MORPHOLOGICAL ANALYSIS OF TEN POPULATIONS OF *PEDICULARIS DENSIFLORA* SUBSP. *DENSIFLORA* AND *P. DENSIFLORA* SUBSP. *AURANTIACA* SAMPLED FROM CALIFORNIA AND OREGON. In all ANOVAs differences among groups had a P-value < 0.05. In Bonferroni (Dunn) t-tests, character means with same letter are not significantly different. Where necessary, data were log, square root, or arccosine transformed, this is denoted below the character as *, † or ‡ respectively.

Character		Lake Santa Margarita (n = 19)	Paradise (n = 50)	Mount Diablo (n = 46)	Bear Valley (n = 50)	Round Valley (n = 51)	Hurles Circle (n = 51)	Missouri Flats Road (n = 50)	McBride Springs (n = 50)	Pinehurst (n = 50)	Inskip (n = 50)
Galea Width*	Mean (SD)	5.27 (0.49)	5.12 (0.44)	5.10 (0.46)	5.31 (0.53)	5.01 (0.52)	5.58 (0.59)	5.68 (0.48)	6.27 (0.64)	6.19 (0.61)	6.46 (0.76)
	Range	4.43–6.56	4.20–6.45	3.99–6.33	4.20–6.53	4.02–6.42	4.37–7.11	4.60–6.64	5.21–8.07	4.89–7.63	.08–8.62
	t-test	C D	D	D	C D	D	B	B C	A	A	A
Tube Width*	Mean (SD)	3.18 (0.31)	3.09 (0.32)	2.99 (0.31)	3.39 (0.39)	3.16 (0.30)	3.39 (0.33)	3.70 (0.35)	4.00 (0.44)	3.81 (0.38)	4.26 (0.48)
	Range	2.75–3.91	2.54–3.88	2.41–3.76	2.67–4.30	2.54–3.69	2.75–4.05	2.89–4.55	3.30–4.94	3.04–4.79	2.97–5.12
	t-test	D E	E	E	D	D E	D	C	A B	B C	A
Galea Length*	Mean (SD)	18.79 (1.41)	18.95 (1.70)	18.98 (1.94)	19.72 (1.69)	19.25 (1.38)	19.07 (1.69)	21.35 (1.64)	20.28 (1.85)	20.41 (1.69)	20.60 (2.08)
	Range	15.39–21.10	15.19–22.20	15.45–22.88	16.39–23.19	16.70–22.40	16.03–22.83	18.00–24.75	16.64–24.87	14.29–24.03	16.50–25.53
	t-test	E	E	E	B C D E	C D E	D E	A	A B C D	A B C	A B
Tube length*	Mean (SD)	10.26 (1.69)	12.83 (1.90)	11.90 (1.52)	15.29 (2.35)	12.56 (1.77)	13.01 (1.83)	14.63 (2.37)	12.81 (1.77)	11.91 (1.41)	14.18 (2.22)
	Range	7.18–13.53	8.90–18.13	7.53–15.27	10.51–20.70	9.38–18.70	9.49–17.85	9.49–20.65	8.60–16.93	9.05–16.45	8.28–19.41
	t-test	D	B C	C	A	C	B C	A	B C	C	A B
Orifice width*	Mean (SD)	11.36 (0.98)	12.30 (1.37)	12.54 (1.63)	12.66 (1.24)	12.45 (1.13)	12.87 (1.39)	14.86 (1.23)	17.52 (1.86)	18.15 (1.59)	17.88 (2.04)
	Range	10.05–13.01	9.86–15.91	9.80–20.01	9.98–15.71	10.33–15.01	10.36–15.99	12.18–17.63	14.57–22.07	13.10–22.28	14.18–23.27
	t-test	D	C	C	C	C	C	B	A	A	A
Calyx Length*	Mean (SD)	13.99 (1.20)	12.67 (1.17)	12.70 (1.41)	14.17 (1.35)	12.39 (1.25)	13.66 (1.45)	13.24 (0.97)	18.83 (2.31)	17.14 (1.77)	18.64 (1.69)
	Range	12.36–16.78	10.13–15.11	10.54–16.78	10.72–17.75	9.83–16.09	10.19–16.35	10.81–15.60	13.08–24.03	11.98–21.10	15.57–22.92
	t-test	C	D	D	C	D	C	C D	A	B	A
Pistil Length	Mean (SD)	25.48 (1.93)	35.44 (4.79)	33.18 (3.52)	38.73 (3.83)	35.92 (2.87)	34.08 (4.50)	37.99 (4.19)	36.62 (3.30)	36.09 (4.63)	37.17 (4.89)
	Range	22.47–29.61	24.67–44.08	25.54–42.01	28.50–46.00	30.44–43.71	24.64–43.29	29.33–48.64	29.74–44.42	17.14–44.73	27.68–46.03
	t-test	E	B C D	D	A	A B C D	C D	A B	A B C	A B C D	A B
Stamen Length*	Mean (SD)	26.42 (3.11)	31.09 (3.45)	28.67 (3.45)	33.29 (3.32)	31.16 (3.01)	31.06 (3.54)	34.46 (3.14)	31.92 (3.02)	31.41 (2.61)	34.13 (3.19)
	Range	16.91–30.95	23.19–38.63	21.45–35.49	24.03–40.28	24.39–39.42	25.18–39.67	27.78–41.66	24.62–41.15	24.09–36.88	26.51–40.94
	t-test	E	C	D	A C	C	C	A	B C	C	A B
Labium Length†	Mean (SD)	3.82 (1.07)	4.09 (0.95)	5.20 (1.32)	5.29 (1.19)	4.65 (0.98)	4.30 (0.91)	5.85 (1.34)	2.87 (0.75)	2.86 (0.70)	3.13 (0.90)
	Range	1.12–5.49	1.84–7.01	3.72–12.23	3.22–8.98	2.88–6.77	2.69–7.44	3.7–12.68	1.30–4.71	1.41–4.24	1.64–5.26
	t-test	D	C D	A B	A B	B C	C D	A	E	E	E
Axis Angle	Mean (SD)	144.56 (12.47)	147.32 (10.86)	145.63 (9.02)	149.90 (10.09)	143.73 (13.98)	149.02 (13.63)	151.57 (10.14)	144.71 (9.90)	143.34 (15.45)	145.90 (11.64)
	Range	123.50–180	122.76–180	125.60–180	121.68–180	99.37–180	118.10–180	132.58–180	117.73–163.88	109.30–180	105.92–167.81
	t-test	A	A	A	A	A	A	A	A	A	A
Tube Exsertion	Mean (SD)	−3.74 (1.94)	0.17 (1.95)	−0.80 (1.54)	1.12 (2.17)	0.16 (1.93)	−0.65 (2.06)	1.38 (2.31)	−6.02 (2.00)	−5.36 (1.76)	−4.46 (2.65)
	Range	−7.14–0.16	−4.12–5.26	−4.76–2.31	−2.99–5.39	−3.76–6.88	−5.74–4.31	−3.05–7.95	−10.33–(−1.63)	−9.62–12.19	−11.25–2.05
	t-test	C	A B	B	A	A B	B	A	E	D E	C D
Corolla Length	Mean (SD)	29.04 (2.33)	31.79 (3.19)	30.88 (2.95)	35.00 (3.35)	31.81 (2.70)	32.08 (3.23)	36.18 (3.61)	33.09 (3.04)	32.32 (2.50)	34.78 (3.02)
	Range	24.80–32.93	25.06–39.71	23.24–37.05	27.98–42.15	27.99–41.10	26.62–39.99	28.60–42.24	25.54–41.80	23.97–38.18	29.33–42.15
	t-test	E	C D	D E	A B	C D	C D	A	C B	C D	A B
Labium Tip to Galea Bend†	Mean (SD)	11.26 (1.41)	10.54 (1.20)	11.64 (1.35)	12.34 (1.28)	11.45 (1.08)	10.51 (1.36)	12.34 (1.28)	5.63 (0.91)	5.11 (0.72)	5.85 (0.84)
	Range	8.90–13.83	8.76–13.07	9.29–14.68	9.48–15.54	8.74–13.69	8.28–13.56	9.90–16.09	3.27–7.28	3.62–6.88	4.48–7.82
	t-test	B C D	C D	A B	A	A B C	D	A	E F	F	E

TABLE 3. CONTINUED

Character		Lake Santa Margarita (n = 19)	Paradise (n = 50)	Mount Diablo (n = 46)	Bear Valley (n = 50)	Round Valley (n = 51)	Hurles Circle (n = 51)	Missouri Flats Road (n = 50)	McBride Springs (n = 50)	Pinehurst (n = 50)	Inskip (n = 50)
Orifice width/ Galea Length‡	Mean (SD)	0.60 (0.05)	0.65 (0.04)	0.66 (0.07)	0.64 (0.05)	0.65 (0.04)	0.68 (0.05)	0.70 (0.05)	0.86 (0.03)	0.89 (0.03)	0.87 0.03
	Range	0.53–0.67	0.55–0.72	0.57–1.07	0.52–0.75	0.58–0.73	0.53–0.79	0.62–0.96	0.79–0.95	0.82–0.96	0.78–0.94
	t-test	E	C D	C D	D	C D	B C	B	A	A	A
Labium Length/ Galea Length	Mean (SD)	0.205 (0.058)	0.216 (0.045)	0.276 (0.073)	0.270 (0.063)	0.242 (0.052)	0.226 (0.042)	0.275 (0.071)	0.141 (0.034)	0.141 (0.035)	0.152 (.044)
	Range	0.060–0.297	0.097–.360	0.166–0.655	0.167–0.525	0.150–0.378	0.147–0.341	0.188–0.690	0.069–0.214	0.060–0.201	0.079–0.239
	t-test	B	B	A	A	A B	B	A	C	C	C
Tube Length/ Galea Length	Mean (SD)	0.548 (0.096)	0.677 (0.081)	0.629 (0.079)	0.777 (0.115)	0.653 (0.080)	0.682 (0.071)	0.682 (0.111)	0.634 (0.084)	0.586 (0.072)	0.696 (0.127)
	Range	0.365–0.744	0.533–0.840	0.479–0.824	0.548–1.106	0.488–0.878	0.489–0.877	0.497–0.977	0.491–0.827	0.437–0.757	0.364–1.042
	t-test	E	B C	C D	A	B C	B C	B C	B C D	D E	B
Tube Width/ Galea Width	Mean (SD)	0.606 (0.056)	0.605 (0.060)	0.589 (0.056)	0.642 (0.072)	0.633 (0.063)	0.611 (0.059)	0.654 (0.070)	0.639 (0.062)	0.618 (0.056)	0.664 (0.078)
	Range	0.474–0.694	0.445–0.739	0.489–0.713	0.481–0.835	0.509–0.762	0.479–0.771	0.501–0.806	0.494–0.747	0.504–0.733	0.466–0.921
	t-test	C D	C D	D	A B C	A B C D	B C D	A B	A B C	B C D	A

Based on the data from the multivariate analysis and ANOVA, and confirmed by observation from 1069 herbarium specimens and field studies several traits are characteristic of *Pedicularis densiflora* and *P. aurantiaca*. Both species are pubescent several-stemmed perennials that grow in diffuse patches, with woody roots and haustoria preferentially parasitizing woody plants. Their leaves are petiolate, oblanceolate, bipinnate to pinnate, and grow in basal rosettes, with alternate branching on the peduncle. The inflorescence of both species is a raceme with flowers subtended by leafy bracts and the flowers have a five lobed calyx and a galeate corolla.

The two species, however, differ in several key character traits. *Pedicularis aurantiaca* has calyces 12–24 mm long and lower labia extending <8 mm from the tip to the galea bend, with the detached portion of the labia 1–5 mm long. The orifice widths are approximately 7/8ths the length of the upper galea, and the detached lower labium to upper galea length ratio is approximately 1:7. Floral tubes are included in the calyx. *Pedicularis densiflora* has calyces 10–18 mm long and lower labia >8 mm from the tip to the galea bend, with the detached portion of the labia 2–12 mm long. The orifice widths are approximately 2/3 the length of the upper galea and the detached lower labium to upper galea length ratio is approximately 1:4. Floral tubes are exserted from the calyx (Fig. 5).

Previous work by Sprague (1958, 1960, 1962) and Macior (1986a) on variation in pollination indicates exclusive pollination by hummingbirds in *P. aurantiaca* and pollination by bumblebees and hummingbirds in *P. densiflora*. Long corolla tubes, abundant nectar, lack of floral scent, and red coloration were floral traits present in *P. densiflora* and *P. aurantiaca* which have an association with hummingbird pollinators (Sprague 1960; Grant & Grant 1968; Faegri and van der Pijl 1966). In *P. densiflora*, young flowers are visited by *Bombus* pollinators before the floral tubes are fully exserted and while the nectar is accessible to the short-tongued pollinators (Macior 1986a). The lower labium of *P. densiflora* was larger and capable of serving as a landing platform for *Bombus* pollinators. In *P. aurantiaca*, the calyx was larger and supported the corolla tube. This trait could serve to protect the ovary during the nectar probing of hummingbird visitation (Faegri and van der Pijl 1966). The labium was also significantly smaller and the orifice width larger in *P. aurantiaca* than in *P. densiflora* flowers. The smaller lower labium in *P. aurantiaca* flowers possibly makes it difficult for *Bombus* pollinators to land and the enlarged orifice width can accommodate the larger head of the hummingbird pollinators.

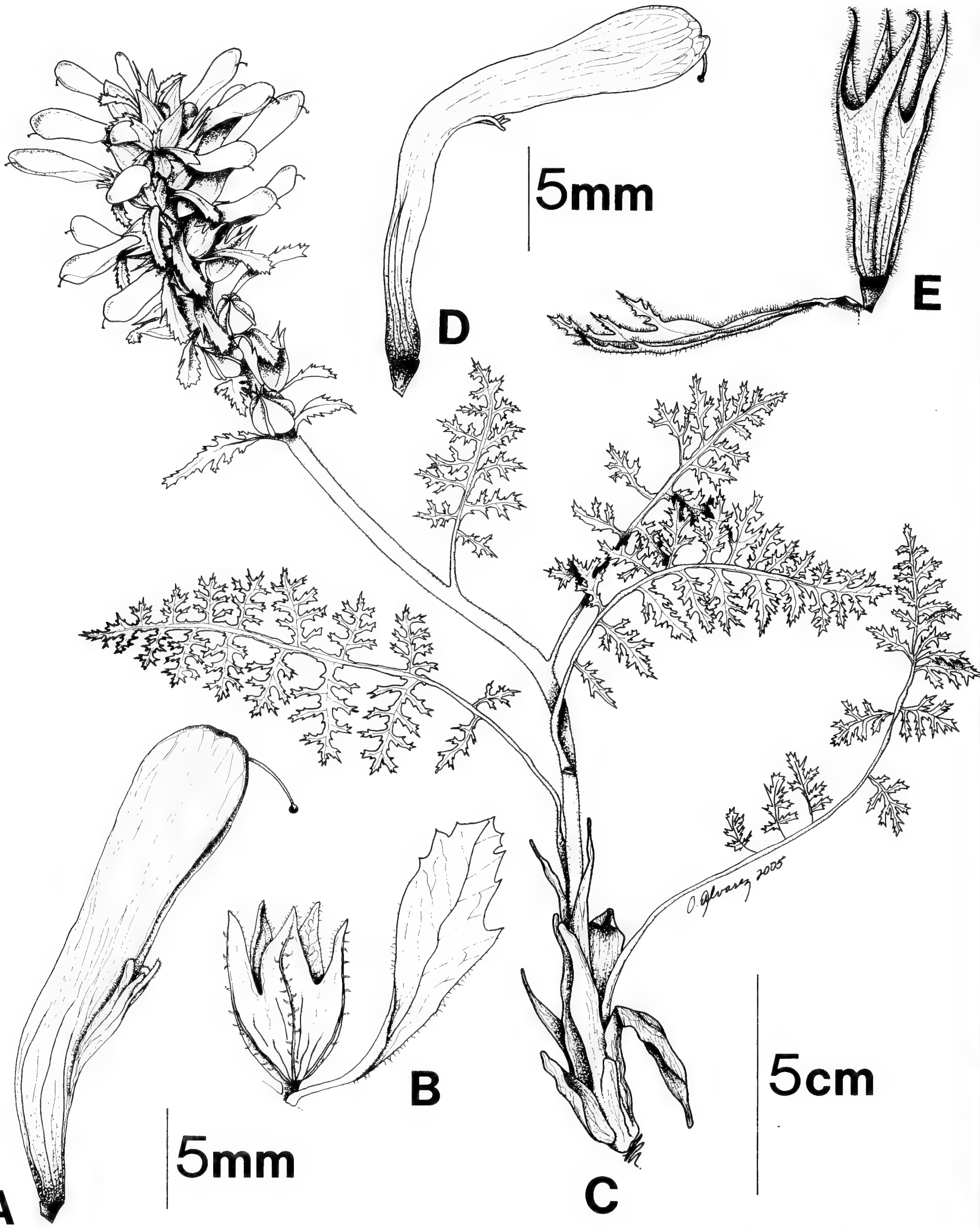

FIG. 5. A. Mature flower minus calyx of *Pedicularis densiflora*. B. Calyx of *P. densiflora*. C. Mature plant of *P. aurantiaca*. D. Mature flower minus calyx of *P. aurantiaca*. E. Calyx of *P. aurantica*. Voucher associated with *P. densiflora* - Monfils 13 (MSC). Voucher associated with *P. aurantiaca* - Monfils 40 (MSC).

KEY:

Corolla ± club-like, upper labium hooded, not beaked; lower labium not fan-like
- Corolla deep red to red-purple (or yellow to orange, occasionally white), lower labium <1/2 upper
  - Lower labium ≥8 mm. Galea opening >4/5th the length of galea. Tube exserted beyond the calyx lobes at anthesis. . . . . *Pedicularis densiflora*
  - Lower labium <8 mm. Galea opening <4/5th the length of galea. Tube inserted in the calyx lobes at anthesis . . . . *Pedicularis aurantiaca*

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Appendix I
Additional Material Seen *Pedicularis aurantiaca*

Additional material seen: *UNITED* STATES. **Oregon:** Jackson County: 1–1.5 mi past Pinehurst Inn. N 42°07.452′, W 122°20.783′, 1167 m, 24 May 1998, *Monfils 12* (MSC); 1–1.5 mi east of Pinehurst Inn. N 42°07.461′, W 122°20.756′, 1131 m, 11 May 2000, *Monfils 40* (MSC); Pinehurst, 20 Jun 1927, *Peck 15044* (DS, WILLU); Pinehurst, 27 May 1948, *Peck 24973* (WILLU, UC); Near Pinehurst, 1219 m, 13 Apr 1934, *Thompson 10347* (CAS, DS, POM, WILLU). Klamath County: Cascade Mnts. Near Long Prairie, along old Klamath Falls-Ashland road, 15 Jun 1895, *Applegate 421a* (DS); Southeast of Topsy, 1372 m, 12 May 1898, *Applegate 2059* (DS); Top of Spencer Mt., Cascade Mts., 11 May 1924, *Applegate 4046* (DS, WILLU); Eastern Cascades, 30 Jun 1902, *Cusick 2851* (DS, ORE, POM); Klamath Falls Road "East of Mt.", 2 Aug 1925, *Henderson s.n.* (ORE); Along Ashland-Klamath Falls road, 18 mi W of Keno, May 1932, *Peck 9302* (DS, WILLU); Mts. Below Klamath Falls near Ore-Calif line, on Klamath River, May 1932, *Sprague s.n.* (OSC). County Unknown: Southern Oregon, 13 May 1907, *Henderson s.n.* (ORE); Location and date unknown, *Bellinger s.n.*, (WILLU). **California:** Amador County: Jackson, 12 Apr 1933, *Ball 18269* (RSA). Butte County: Colby, May 1890, *Austin 111* (UC); Jonesville, 16 Jun 1923, *Bassett s.n.* (CAS); Paradise, May 1898, *Bruce 2419* (DS, POM); Brush Creek, 1907, *Conger 453* (CAS, POM); Chico Meadows in the Sierra Nevada, 1219 m, 11 Jun 1915, *Heller s. n.* (DS); Stirling, 1073 m, 18 May 1919, *Heller 13170* (CAS,DS); Pentz Road, 3 mi below Paradise, 23 Mar 1939, *Heller 15358* (DS); DeSabla, 853 m, 18 Apr 1978, *Howell 52852* (CAS); Above the road between Paradise and Butte Meadows .1 mi. s. of Inskip. T25N, R.4E, sect. 33, 10 May 1981, *McNeal 2487* (OSC); Inskip on Skyway Road. Elevation N 39°59.541′, W 121°32.389′, 1309 m, 22 May 1998, *Monfils 6* (MSC); Inskip on Skyway Road. N 39°59.527′, W 121°32.461′, 1309 m, 9 May 2000, *Monfils 37* (MSC); Durham, 17 Apr 1932, *Morrison s. n.* (CAS). Fresno County: 5 mi east of Auberry, Big Sandy Bluff, 945 m, 19 Mar 1969, *Ahner s. n.* (CAS); Big Sandy Valley near the foot of ne. slope of Black Mnt. Big Sandy Bluff beyond Ridge View Ranch which is across the road from my place, 610 m, 20 Mar 1953, *Carter 157* (CAS, UC); About 2 mi north of Kerckhoff Resevoir, 610 m, 29 May 1967, *McClintock*, *Roderick &.Johnson s. n.* (CAS); Old fire trail road off Auberry Road. N 37°05.144′, W 119°26.859′, 1147 m, 20 May 1998, *Monfils 4* (MSC); R. R. Grade Rd. 1+ m. w. of jct. Hiway 168 at Shaver Xing between Shaver L. & Big Crk. 1st live crk. – small intake with pipe heading down crk. – Big Creek pentstocks in view. Heavy yellow pine for. 4500'–1000' up s. wall Big Crk. Canyon; 6830' Music Mt. Just sw; 8107' Black Pt. N. across canyon, San Joaquin R. at 2000' 4 map miles w., 17 Jun 1955, *Quibell 5102* (RSA); 5 mi east of Auberry, Big Sandy Bluff range, 945 m, 19 Mar 1969, *Shannon s. n.* (RSA); Scattered along Old Railroad Grade Road. R.23E., T9S., SW1/4 section 34, 853 m, 22 Mar 1980, *Shevlock 6819* (CAS, MSC); Taken near Fish Camp, 14 Apr 1938, *Whilton s. n.* (RSA); Along road from Shaver Lake to Big Creek Power House. W. slope of Sierra Nevada, 1829 m, 5 May 1929, *Wolf 3682* (RSA); 6 mi. above Auberry on road to Pineridge. W. slope of Sierra Nevada [Editorial comment: Georeferenced in Madera County], 18 May 1933, *Wolf 4786* (CAS, RSA, UC). Kern County: Poso Creek narrows, below Poso Flat, 762 m, 9 Mar 1963, *Record 82-1* (CAS-2); Near mouth of South Fork Kern River Canyon, trail along Bartolas Creek, Domeland Wilderness, north of California highway 178 and NW of the Bloomfield Ranch. R35E, T25S, section 23. Lat/Long: 35 degrees 44′45″N, 118 degrees 11′15″W., 1006 m, 20 Apr 1991, *Shevock 12026* (CAS); Back canyon at the cypress grove, 1265 m, 26 May 1964, *Twisselmann 950* (CAS-2). Mariposa County; Mariposa, 610 m, 10 Apr 1959, *Ballantyne 236* (CAS); Awahnee, 9–16 Apr 1926, *Shank 17471*, (RSA). Placer County: Tahoe Forest, Rebel ridge Range [Editorial comment: Georeferenced in Sierra County], 701 m, 12 Apr 1926, *Smith 53916* (CAS-2). Plumas County: Sw. shore Lake Almanor, 2 mi. s. of jct. of State Hwys. 89/36, 1402 m, 23 May 1957, *Balls 22519* (RSA, UC); 1 3/10 s. of Drakesbad, 3 Jul 1938, *Cantelow 2323* (CAS); Prattville, Summer 1906, *Coombs s. n.* (CAS); Woodleaf, 3000–4000', 14 Apr 1931, *Rose s. n.* (CAS, DS, POM, UC); Lake Almanor, 4300', 30 May 1957, *Sprague 1214* (RSA); Growing in dry loam in shade of *Libodedrus decurren*, A low cool draw 6 mi south-west of Viola, 2800', 30 May 1957, *Sprague 1231* (RSA). Shasta County: Montgomery Creek, 18 Apr 1923, *Beltiel s. n.* (CAS); Near McBride Springs. On banks and under chaparral [Editorial comment: Georeferenced in Siskiyou County], 24 Jun 1938, *Cooke 11098*, (DS, OSC); Squaw Creek Ranger Station, Jun 1916, *Drew s. n.* (DS); Mt. Shasta [Editorial comment: Georeferenced in Siskiyou County], 21 Jun 1893, *Dudley s. n.* (DS); Burney Butte, 12 Jul 1912, *Eastwood 1034* (CAS); Shasta Springs [Editorial comment: Georeferenced in Siskiyou County], 20 May 1923, *Eastwood 11854* (CAS-2); Shasta Springs [Editorial comment: Georeferenced in Siskiyou County], 15 May 1918, *Herrin s. n.* (CAS); Shasta Springs [Editorial comment: Georeferenced in Siskiyou County], May 1922, *Herrin s. n.* (CAS); Open manzanita-oak association 3 mi east of Redding, 500', 17 May 1940, *Hitchcock 6466* (DS, POM); Highway 44, 5 mi west of Lassen National Park, 4600', 9 May 1974, *Keller 1301* (CAS). Siskiyou County: Bare serpentine gravel hillside, Scott Mnt. 8 mi above Callahan, 5150', 17 May 1954, *Barneby 11537* (CAS); Near Mt. Shasta, 6000–7000', 1–15 Jun 1897, *Brown 356* (DS); Alpina Mnts. Goosenest foothills, 5000', 10 May 1910, *Butler 1324* (DS, POM, UC); N. slope of Scott Mnt., 4000', 20 May 1936, *Cantelow 1435* (CAS); Scott Mountain campground, 10 mi S. of Callahan, 5350', 21 May 1949, *Constance, Bonar, Holm & Wood 3288* (UC); 0.8 mi N of Scott Mnt. Summit on Hwy 3. South Slope, 5200', 5 Jun 1975, *Davidson 2684*, (RSA); Bald mountain in road from Mt. Hebron to Montague, 5500', 15 May 1940, *Gould 1242* (DS); Mt. Eddy in open gravelly places in the forest, 6800', 15 Jul 1915, *Heller 12085* (CAS,DS, UC); Sugar Creek, Salomon Mountain Range, 5500', 26 May 1949, *Parker 257* (UC); Weed, 10 Apr 1913, *Smith 66* (CAS); Dunsmuir, 29 Apr 1913, *Smith 151* (CAS); Shady hillside near Weed, 28 Mar 1930, *Tebbe 61* (UC); Salmon Mnts., Klamath National Forest. Near South Fork of Salmon River, 5 to 9 mi southeast of Cecilville, between Lat. 41°03′ and 41°06′N., and Long 122°58′ and 123°03′W. Vicinity of Blind Horse Creek, 3000–3500', 13 May 1954, *Thomas 4129* (DS-2); Salmon-Trinity Mnts. about 6 mi SE of Cecilville. West side of Rush Creek, 3800–

4000', 21 Jul 1954, *Thomas & Thomas 4425* (DS); Mt. Shasta, McBride Springs. N 41°20.687′, W 122°16.506′, 4922', 11 May 2000, *Monfils 43* (MSC). Tehama County: Along road from Viola to Mineral, 9.5 mi south of Viola, 5000', 12 Jun 1962, *Breedlove 3423* (CAS, DS); Deer Creek Rd. (Rt. 32) at milepost 12, E side of Deer Creek ca 20 airmiles SW of Chester, 3200', 3 May 1989, *Ertter 8435* (RSA); Mill Crk. Meadows, 6 Jun 1951, *Quick 51-93* (CAS); Northern Sierra Nevada. Red Bluff – Susanville Road. 3 6/10 mi. below Mineral, 4800', 17 May 1937, *Wolf 8712* (RSA). Trinity County: T35N, R11W, sect. 6. North fork of Trinity River, Hobo Gulch Camp and Vicinity. (18 mi NW of Weaverville) Along East Fork Trail, just over on the east side of Backbone Ridge, 4000', 25 Apr 1972, *Carter 374* (CAS-2); T36N, R11W, sect. 31. North fork of Trinity River, Hobo Gulch Camp and Vicinity. (18 mi NW of Weaverville) Along trail 0.1 mi north of Hobo Gulch. (Same location as 399-27 Apr. 72), 3100', 8 Jun 1972, *Carter 399.01*, (CAS-2); Scott Mnts. N. of Carrville, 25 Jun 1937, *Eastwood & Howell 5013* (CAS); 3 mi from Douglas City on Redding Road, 26 Apr 1954, *Howell 29164* (CAS); Dry open coniferous forest in Canadian Zone, Scott Mt. Summit on road from Carrville to Callahan, 5400', 20 May 1980, *Howell, Fuller & Barbe 53541* (CAS); Weaverville, Spring 1915, *Junkans s. n.* (CAS); Trinity Center, 30 Apr 1928, *Kildale 4605* (DS); Weaverville, 30 May 1931, *Kildale 10812* (DS); Foothills, Weaverville, 4000', 11 Apr 1880, *Kleiberger s. n.* (CAS); East Weaver Campground on East Weaver Creek Road. N 40°46.399′, W 122°55.371′, 4248', 23 May 1998, *Monfils 8* (MSC); Hobo Gulch. N 40°55.723′, W 123°09.398′, 4249', 23 May 1998, *Monfils 9* (MSC); East Weaver Public Camp, East Weaver Creek, 3000', 16 May 1949, *Munz 13256* (RSA); T32N, R9W, Secs. 28 & 33; Mt. Diablo Meridian; Southeast of confluence of Panwauket Gulch and Reading Creek; blue oak-pine woodland, 610 m, 18 May 1975, *Sullivan 88* (RSA); Little East Weaver Creek, 3000', 21 May 1914, *Yates 19370* (CAS). Tulare County: Mineral King, 2000', 11 Apr 1958, *Pawek 418* (DS); Occasional in recently disturbed road bank along Blue ridge, section 10, R.29E., T. 19S. South facing slope, 4900', 12 May 1979, *Shevock 6186* (CAS); Uncommon along Calif. Hwy 245, about one mile west from the junction with Dry Creek Road. R.27E., T.15S. section 15, 2800', 11 Mar 1980, *Shevock 6775* (CAS); Lone Pine Spring, White River, 3350', 8 Mar 1940, *Smith 51*, (CAS). Tuolumne County: Priest Grade, near Big Oak Flat, Yosemite National Park, 20 Feb 1982, *Botti 1489* (CAS). Groveland. Woodland edge of route 120 about 4 mi east of town, 23 Apr 1974, *Churchill 744231* (MSC). Yuba County: Between Dobbins and Bullard Bar Dam, Watershed of North Fork of the Yuba River, 3.1 mi. e. of Dobbins (or 5.5 mi s.w. of Bullard Bar Dam), 2570', 19 Apr 1956, *Bacigalupi, Robbins & Chisaki 5622* (RSA); Comptonville, 7 Apr 1918, *Eastwood 6795* (CAS). County Unknown: Sterling City, 18 May 1935, *Whitaker s. n.* (OSC).

Appendix II
Additional Material Seen *Pedicularis densiflora*

Additional material seen: UNITED STATES. **Oregon:** Jackson County: Thompson Creek, near Applegate, steep hill slope. sect. 21 T.38S R.4W, 1400', 19 Mar 1940, *Detling 3864* (ORE); Fls. Deep purple-red open pine woods on alluvium, along Applegate River, 11/2 mi. s.e. of Provolt, 28 Apr 1948, *Glowenke 11113* (UC); 5 mi S of Applegate, under madronas, 1 Jun 1951, *Hitchcock 19395* (RSA); Applegate Creek, Mar 1921, *Leiberg s. n.* (ORE); Applegate R., Jacksonville, 27 Mar 1936, *Lund s. n.* (OSC); Pilot Rock, 20 Apr 1932, *Neiman s. n.* (WILLU); Woods along Thompson Cr. 5 mi. S. of Applegate P.O., 26 Jun 1931, *Peck 16423* (WILLU-2); Along the Applegate River, 12 Apr 1927, *Thompson 2225* (DS,ORE). Josephine County: 4 mi. N.W. of Provost, 25 Apr 1943, *Bellinger s. n.* (WILLU); 3 mi south of Grants Pass on New Hope Road, 9 May 1963, *Curtis s. n.* (OSC); Applegate Valley T37S R5W sect. 34, 21 Apr 1942, *Detling 5138* (ORE); In open woods, Fruitvale, 21 Apr 1930, *Henderson 12513* (ORE); Roadside in mixed Oak-Pseudotsuga woods; S. facing; on old river bench. 2 mi E of Murphy R5W; T37S; SE1/4 OF NW1/4, 345 m, 20 Apr 1968, *Lillico 426* (ORE); Missouri Flat Road. N 42°19.288′, W 123°13.871′, 3900', 24 May 1998, *Monfils 13* (MSC); Missouri Flat Road. N 42°19.288′, W 123°13.871′, 3900', 10 Apr 1999, *Monfils 36* (MSC); Applegate River, North Bank Road c. I mi. from Redwood Highway; S. of Grants Pass, 1300', 23 Apr 1967, *Pike 111* (ORE); Hillside near Grants Pass, 19 Mar 1918, *Prescott s. n.* (WILLU); Near Williams Creek highway between Provolt and Williams; also on N. side of Applegate River on Missouri Flat. Clayey soil in woods, 13 Apr 1924, *Savage s. n.* (ORE); Fruit Dale, Murphy Road. In open woods, 24 Mar 1926, *Savage s. n.* (ORE); Mixed woods near Takilma, 21 Apr 1930, *White s. n.* (ORE). **California:** Alameda County: Laundry Harm, 29 Jan 1895, *Cannon s.n.* (CAS); Oakland Hills, 28 Feb 1936, *Covel 371* (CAS); Laundry Harm, 26 Apr 1891, *Eastwood s.n.* (ORE); Mines Road s. w. of Livermore, near entrance to Rancho Los Mochos Boy Scout Camp, 1500', 3 Mar 1968, *Gagné s.n.* (CAS). Butte County: Near Hurleton, 1800', 26 Mar 1980, *Ahart 2060* (CAS); Cherokee mine, 29 Mar 1919, *Heller 13097* (CAS, DS, POM); Hurles Circle, in center island. N 39°29.764′, W 121°22.632′, 2050', 22 May 1998, *Monfils 5* (MSC); Hurles Circle, in center island. N 39°29.764′, W 121°22.632′, 2050',7 Apr 1999, *Monfils 35* (MSC). Calavaras County: Comanche, 16 Apr 1939, *Hoover 4032* (CAS). Colusa County: Wilbur Springs. T15N, R6W, sect. 35, 3500', 14 Apr 1979, *Roth 9* (RSA); Along Brim Rd., 2.9 mi. W jct. Bear Valley Rd., 30 Mar 1996, *Vincent & Rhode 7304* (RSA). Contra Costa County: Martinez, 300', 18 Mar 1931, *Benson 2662* (POM); Mount Diablo, 17 Mar 1922, *Eastwood 11084* (CAS); Rocky Point, Mount Diablo. N 37°51.814, W 121°55.770′, 2550', 22 Mar 1999, *Monfils 28* (MSC); Rocky Point, Mount Diablo, 2000', 5 Apr 1956, *Sprague 1096* (RSA); Mount Diablo, 2000', 11 Apr 1957, *Sprague 1124* (RSA); Rocky Point, Mount Diablo, 2000', 30 May 1957, *Sprague 1134* (RSA). Glenn County: 2 mi north of Alder Springs, 3900', 19 May 1949, *Munz 13330* (RSA). Humbolt County: T7N, R5E, sect. 29. Along highway 96, 1.9 mi north of Willow Creek, 1 May 1965, *Anderson 3556* (RSA); In damp fir woods near creek, Boise Creek and Willow Creek, Trinity River, 1 Apr 1947, *Brown 25* (DS); Philabiumsville, south fork of El River, 20 Mar 1927, *Kildale 2909* (DS); Briceland Bridge near Garberville, 375', 17 Apr 1925, *Kildale 3096* (DS, RSA); Briceland Road. N 40°05.678′, W 123°51.222′, 1874', 25 May 1998, *Monfils 14* (MSC); Round Valley Historical Marker. N 39°43.749′, W 123°15.112′, 2160', 25 May

1998, *Monfils 16* (MSC); Kneeland Prarie, in woods in ravine, 2500', 8 Jun 1908, *Tracy 2637* (UC); Vicinity of Garberville, 400', 17 Mar 1923, *Tracy 6160* (UC); Trinity River Valley, near the south fork, 600', 28 Feb 1926, *Tracy 7369* (UC); Hoopa Mnt., near summit on road west from Hoopa to Bair's, 3500', 15 May 1927, *Tracy 8060* (UC); Willow Creek Canyon, 2000', 26 Apr 1931, *Tracy 9340* (UC); Trinity River Valley, at Willow Creek, 500', 3 Apr 1937, *Tracy 15251* (UC); Trinity River Valley, at Willow Creek, 500', 26 Mar 1941, *Tracy 16818* (UC); Harris, in woods, 2500', 31 May 1948, *Tracy 18006* (UC). Lake County: Lakeport, 20 Apr 1917, *Bentley s. n.* (DS); Mt. Kelseyville, Middle N. Coast, Near Cold Creek Canyon River, 1700', 30 Mar 1928, *Benson* 87 (POM); Bogg's Lake, Mt. Hanna, Middle N. Coast, Clear Lake watershed, 3500', 18 May 1935, *Benson 6636* (POM); Hannah, 3000', 8 Apr 1923, *Blankinship s. n.* (CAS); Mt. Konocti, 2000', 27 Mar 1926, *Blankinship s.n.* (RSA); Sulphur Banks, Apr 1902, *Bowman s. n.* (DS); E. of Middleton, 7 Apr 1940, *Cantelow 4346* (CAS); 4 mi. below Tollhouse on Middleton Road, 22 Feb 1924, *Duncan s. n.* (DS); Dasheills Mt., Sanhedrin, 23 May 1925, *Eastwood 12912* (CAS); Elk Mt., 17 May 1938, *Eastwood & Howell 5703* (CAS); Clear Lake, 14 Apr 1928, *Galloway s.n.* (CAS), Glenbrook, near Jordan Park, 30 Mar 1931, *Jussel 29* (CAS); Cobb Mt., 30 Mar 1931, *Jussel s. n.* (CAS); Cobb Mt., 31 Mar 1931, *Jussel s. n.* (CAS); Mt. St. Helena, 1 Apr 1933, *La Motte s. n.* (POM); Cobb Mt., 4 Jul 1893, *Leitholt s. n.* (DS); Bear Valley on Brim Road. N 39°09.504′, W 122°28.778′, 2665', 26 May 1998, *Monfils 17* (MSC); Bear Valley on Brim Road. N 39°09.431′, W 122°28.798′, 2180', 26 May 1998, *Monfils 33* (MSC); Butt's Cyn. Rd. near Middleton, 1000', 25 Mar 1972, *Shevock 1437* (RSA); Northeast facing slope, 0.4 mi southeast of Black Oak Villa in Butts Canyon, 1.1 mi from Lake-Napa county line on Pope Valley road, 800', 7 Mar 1953, *Sweeney 971* (UC); Chaparral 11 mi. S. of Lower Lake, 13 Mar 1932, *Wiggins 5769* (DS); 21/2 mi S. W. of Lakeport. sect. 34, T.14N, R.10W, 1850', 14 May 1937, *Wilson 376* (UC). Los Angeles County: Mts. above Claremont, Johnson Pasture, 15 Feb, *Bragg s. n.* (POM); North slope Sta. Monica Hills, Feb 1903, *Braunton 809* (DS, ORE-2); Topanga Canyon, 28 Mar 1929, *Clare s.n.* (RSA-2); Laurel Canyon, 24 Feb 1929, *Detruers s.n.* (RSA); Mulholland Drive, 6 Mar 1935, *MacFadden13246* (CAS); Laurel Canon, Mar 1943, *Merritt s.n.* (RSA); Franklyn Canyon, Santa Monica Mts., 21 Feb, *Peirson 1168* (RSA); Glendora, Little Dalton Trail, 16 Feb 1916, *Perkins s.n.* (RSA); 0.7 mi from Triunfo Canyon, 2 mi west of Cornell, Lobo Canyon, 800', 31 Mar 1959, *Thompson 1010* (CAS, RSA); Hwy. 23 south of Lake Elanor, Santa Monica Mtns., 1000', no date, *Wallace & Wilkin 150* (RSA). Marin County: East side of the Tiburon Peninsula just below the summit, 31 Mar 1981, *Best s. n.* (CAS); On trail 0.5 mi. above Phoenix Lake near jct. of Mt. Tamalpais trail, 1200', 5 Apr 1956, *Campbell 8* (RSA); Mount Tamalpais, 22 Feb 1901, *Chandler 760* (POM, UC); Old hardpacked fire road, 100', 9 Feb 1975, *Edelbrock 4*, (CAS); Summit Alpine Lake Trail above Deer Park, 8 Mar 1936, *Ewan 9408* (RSA); Summit Alpine Lake trail above Deer Park, 8 Mar 1936, *Ewan 9409* (UC); Mt. Tamalpais, 22 Apr 1930, *Forest s. n.* (RSA); Tamalpais T1N R6W, 600', 28 Mar 1935, *French 619* (UC); South side of Mt. Tamalpais, 7 Mar 1902, *Heller & Brown 5008* (DS, MSC, POM); Tiburon, 15 Feb 1938, *Hoover 2739* (UC); San Geronimo Ridge, 25 Feb 1940, *Howell 15388* (CAS); Carson Ridge, 19 Apr 1942, *Howell 16949A* (CAS-2); San Arseloro Canyon, 25 Feb 1940, *Howell s. n.* (CAS); Above Blythedale Canyon, east side of Mt. Tamalpais, 2 Mar 1947 *Howell s. n.* (CAS); Mill Valley, 29 Mar 1891, *Jepson s.n.* (UC); Alpine Dam Road, about 1 mi from Alpine Gulch on Fairfax side, 1040', 10 Mar 1968, *Kawahara 29* (CAS); Marin County, 1868–1869, *Kellogg & Harford 713* (CAS); Ross Valley, Apr 1892, *Michener & Bioletti s. n.* (MSC); Tamalpais, Apr 1892, *Michener & Bioletti s. n.* (MSC); Fire road, south side of Mount Tamalpais, 12 Apr 1969, *Mitchell 4* (OSC); Paradise Beach Park, Tiburin Uplands Nature Preserve. N 37°53.329′, W 122°26.954′, 109', 26 May 1998, *Monfils 18* (MSC); Paradise Beach Park, Tiburin Uplands Nature Preserve. N 37°53.309′, W 122°27.055′, 137', 3 Apr 1999, *Monfils 34* (MSC); Mt. Tamalpais, 3 Mar. 1930, *Morris s. n.* (RSA); Rcky and clayey bank by Paradise Dr., 0.7 mi. N. Paradise Beach Park, Tiburon Peninsula, 10 Apr 1975, *Norris 2305* (RSA); Tiburon Peninsula, 200', 15 Mar 1930, *Parks 402* (POM, UC); Tiburon, Spring 1926, *Parks* (UC); Alpine Dam Road above Fairfax, 800', 9 Mar 1963, *Sharsmith 5194* (UC); Corte Madera, 1 Mar 1903, *Sheldon 11563* (ORE); Phoenix Lake, Ross, 1000', 4 Apr 1956, *Sprague 1096* (RSA); Carson Ridge, 4 Apr 1957, *Sprague 1120* (RSA); Fairfax, Mar 1928, *Suttliffe s. n.* (RSA); North slope of hill near Forest Knolls, 21 Mar 1936, *True s. n.* (RSA); Phoenix Lake, Ross, 1000', no date, *no collector* (RSA); Mt. Tamalpais, Apr 1898, *no collector* (CAS). Mendocino County: Abt. 12 mi. e. of U.S. 101, along Calif. 20. In shade above road, 6 Apr 1954, *Clarkson 300* (OSC); Red Mnt., n. Mendocino Co., 21 Jun 1937, *Eastwood & Howell 4663* (CAS); Near Woodville, May 1889, *Howell s. n.* (UC); Ukiah, 25 Apr 1924, *Jones s. n.* (DS-2, POM); Kaiser District, Mar 1903, *McMurphy 306* (DS); 8 mi north of Ukiah, 6 Apr 1938, *Meyer 1384* (UC); Round Valley Historical Marker. N 39°43.749′, W 123°15.112′, 2160', 25 May 1998, *Monfils 16* (MSC); Round Valley Historical Marker. N 39°43.760′, W 123°15.093′, 1966', 29 Mar 1999, *Monfils 32* (MSC); Mad River, 6 Jul 1890, *Price s. n.* (UC); Potter Valley, Apr 1894, *Purpus 1009* (UC); Shady Hills, n. Potter Vall., Mar 1894, *Purpus 3089* (UC); Along rte. 128 at MP24.26, 400', 5 Mar 1979, *Smith & Wheeler 5128* (CAS); Red Flat, ¼ mi. from wooden gate btwn, BLM & Coombs property. Red Mnt. N., 2350', 6 Jul 1981, *Smith et al. 6855* (CAS); Summit area of Red Mountain North, 7 Jul 1981, *Smith et al. 6868* (CAS); Seven miles north of Laytonville near highway 101, 20 Apr 1968, *Thomas 14331* (DS); Rte. 253. South of Robinson Creek Rd., Ukiah, 650', 11 Mar 1978, *Wheeler 60* (CAS); South of Leggett on the Old Redwood Hwy, 1000', 1 Feb 1980, *Wheeler 1298* (CAS); Round Valley Historical Marker, overlooking Covelo on Hwy. 162, 2000', 12 Apr 1979, *Wheeler & Smith 905* (CAS); Little River – Albion Road. Near Little River Airport, 600', 23 May 1979, *Wheeler & Smith 1026* (CAS); On Northwesterly slope, 4 mi east of Laytonville, along road to Dos Rios, 20 Mar 1948, *Wiggins 11587* (DS, RSA). Monterey County: Gravel Pitt Hill, 27 Jun 1905, *Dudley s. n.* (DS); Monterey, 1874, *Abbott s. n.* (CAS-2); Carmel Highlands, Peter Pan Rd., 200', 21 Feb 1948, *Balls 7834* (RSA); Monterey, 29 Mar 1933, *Detling 1108* (ORE); Pine Cañon, 1500', 27 Mar 1920, *Duncan 86* (DS); Near Cypress Pt., 28 May 1912, *Eastwood 94a* (CAS); Pacific Grove, 8 Mar 1923, *Eastwood 2471* (CAS); Monterey, 9

Mar 1913, *Eastwood 2489* (CAS); Pacific Grove, Apr 1902, *Elmer 3543* (DS-2, POM, UC); Two miles south of Jolon on hilltop, 10 Mar 1952, *Evans s. n.* (CAS); Sand Stone Cliffs near north fork of San Antonio River, 1500', 27 Mar 1920, *Ferris 1810* (DS); Landels-Hill Big Creek Reserve, Gamboa Point Section, Santa Lucia Mountains, sect. 4, 2 Apr 1982, *Genetti & Engles 48* (CAS); Del Monte Forest, Pacific Grove, 1 Apr 1955, *Howitt 132* (CAS); Pacific Grove, 12 Apr 1933, *Jussel s. n.* (DS); Summit of Hesperia Mountain, north of Bryson, southern Monterey County, 1550', 2 May 1933, *Keck 2093* (DS-2); Near the school, Francis Simes Hastings Natural History Reservation, Santa Lucia Mts., 2 Apr 1944, *Linsdale 71* (CAS); Santa Lucia Mountains, Apr 1898, *Plaskett 75* (UC) Carmel-by-the-Sea, 3 Mar 1910, *Randell 53* (DS); By trail from Carmel to Monterey, 30 Dec 1909, *Randall s. n.* (DS); Parkfield Road, 1.5 mi east of Vineyard Canyon Summit, 2200', 4 Apr 1956, *Twisselmann 2618* (CAS-2); Del Mouh ur. Salinias Road, 15 Apr 1912, *Woodcock s. n.* (POM). Napa County: Mt. St. Helena Trail, 4 May 1928, *Abrams 12265* (DS); Summit of St. Helena Grade, 3 May 1928, *Abrams s. n.* (DS); Howell Mt., 22 Mar 1936, *Cantelow 1142* (CAS); East slope in the Howell Mountains, 5 mi east of Napa, North Coast Range, 1500', 27 Mar 1938, *Constance 2036* (DS, UC); Northern exposure above Putah Creek, along State Hwy. 128, about 6 mi east of Monticello, 26 Feb 1953, *Crampton 989* (UC);7.2 mi from St. Helena on road to Pope Valley, 2 Apr 1950, *Finfrock 17* (UC); Wooded slope in the oak belt about 5 mi south of Calistoga, 12 Apr 1924, *Heller 13840* (DS, POM); Near the summit of the ridges east of Napa on the Monticello road on a clay bank among shrubs, 12 Mar 1940, *Heller 15514* (DS); Wooden Valley road, east side of Napa Range, 8 mi from Napa, 2 Apr 1931, *Keck 1030* (DS, POM); Calistoga, 13 Apr 1929, *Linsdale 257* (UC); Old Howell Mountain Road, 1500', 31 Mar 1967, *Muth 596* (RSA); 1 mi from Pacific Union College, beside road to Pope Valley, 1 May 1949, *Popenoe 18* (OSC); Hills just n. of White Sulphur Ck., w. of Saint Helena, 500', 22 Feb 1954, *Raven s. n.* (CAS); Base of Mt. St. Helena, 3 May 1928, *Wolf 1845* (DS); Summit of Mt. St. Helena Grade, north of Calistoga, *Wolf 1845* (RSA); Upper slopes of Mt. St. Helena, 4 May 1928, *Wolf 1856* (RSA). Nevada County: American Ranch Hills, 5 mi south-west of Grass Valley, on McCourtney Rd., 2200', 8 Apr 1962, *True 356* (CAS). Orange County: 14.3 mi east of San Jaun Capistrano on State 74, 1100', 9 Mar 1962, *Breedlove 1789* (DS); Santa Ana Mountains, Cleveland Nat. Forest. Pleasants Peak (on Orange-Riverside Co. line), 4000', 18 May 1977, *Davidson 5601* (RSA); Sitton Peak Truck Trail: 0.3 mi W of ranger station near hot springs, on Ortega H'way (SR 74), 25 Apr 1990, *Jaroslow B36* (RSA); Sierra Peak Trail, Santa Ana Mts, 11 Apr 1929, *Johnson 1259* (RSA); 5 mi east of Trabuco Oaks, Trabuco Canyon, Cleveland National Forest, 1300', 6 Apr 1966, *Lathrop 6142* (RSA). Riverside County: Santa Ana Mountains, 3 mi above De Luz on dirt road, 3000', 30 Apr 1966, *Adams s. n.* (RSA); Vail Lake area, summit of "Big" Oak Mtn, N. of lake. T7S, R1W, SW ¼ sect. 34. Saddle between summits, N slope along rd heading N to Black Hills, 2600', 30 Mar 1990, *Boyd, Ross & Arnseth 3944* (RSA); Vail Lake area, saddle at N base of "Big" Oak Mtn, S of Black Hills. T7S, R1W NE ¼, SW ¼ sect. 34, 2400', 30 Mar 1990, *Boyd, Ross & Arnseth 3953* (RSA); Santa Ana Mountains, San Mateo Cyn. Wilderness Area. Tenaja Trail from jtn. W/ Morgan Tr. S to Pigeon Spring area. T6S, R5W sect. 32; T7S, R5W sect. 5, 2200–2600', 31 Mar 1992, *Boyd, Ross & Arnseth 6763* (RSA); Aguate, So. Calif., 7 Apr 1929, *Clarkk 2035* (RSA); Corona Skyline Drive, Santa Ana Mts. So. Calif., 7 Apr 1929, *Crow 304* (RSA); Vicinity of Beaumont, 17 Apr 1897, *Hall 476* (UC); Aguanga, 22 Dec 1925, *Jaeger s. n.* (POM); Corona, sect. 22, T4S, R7W, 2800', Mar 1934, *Jensen 318* (UC); 18 mi S. W. of Elsinore. South slope of Tenaja Canyon, 2 Apr 1959, *Lathrop 4408* (RSA); 4 mi west of Corona between Tin Mine Canyon & Santiago Peak, Skyline Drive, 4000', 9 Apr 1969, *Lathrop 6968* (RSA); Beaumont, 2000', 25 Mar 1919, *Munz, Street & Williams 2327* (DS, POM); 4 mi. SE of Oak Flat near west county line on Santiago Pk. Fire road near top of peak west of Santiago Pk., Santa Ana Mts., 4200', 14 Apr 1959, *Olmsted 374* (RSA); Along roadside in red clay soil, about 4 mi west of Beaumont, on road to Redlands, 19 Mar 1921, *Peirson 2741* (RSA); Rancho Calif. area, ca. 8 mi. (airline) NW of Temecula, between Bruce Lane & Via View Dr. (T 7S, R 1W SBBM NW /4 of SW /4, sect. 27), 2400', 22 Feb 1988, *Pendelton s. n.* (RSA); Santa Ana Canyon, Santa Ana Mountains, 15 Apr 1922, *Pierce s. n.* (POM); 1 mi south of Aguangam, Hwy 79, Agua Tibia Mts., 1940', 12 Apr 1951, *Rush 169* (POM-2); In herbosis, Lambs Canyon proper, Banning, 2300', 25 Apr 1922, *Spencer 1910* (RSA). San Benito County: Eastern exposure on Peak Trail, Pinnacles National Monument, Paicines, 1500', 22 Mar 1955, *Burgess 84* (UC); Pinnacles Nat. Mon., 550 m, 6 Jun 1931, *Fosberg 35251* (RSA); North slope, the Pinnacles, 29 Mar 1930, *Howell 4611* (CAS); Pinnacles National Monument, High Peaks Trail. N 37°53.386′, W 122°26.991′, 107', 27 May 1998, *Monfils 20* (MSC); Pinnacles National Monument, 1600–1700', 11 May 1940, *Pennell & Powell 25370* (UC); Pinnacles National Monument. Pinnacles Loop Trail, 1200–2500', 27 April 1975, *Thomas 17828* (DS). San Bernardino County: Devore near San Bernardino, 1900', 12 Mar 1928, *Feudge 1960* (POM); Foothills San Bernardino Mts., Apr 1882, *Parish 707* (DS, ORE, UC). San Diego County: Santa Ana Mtns, San Mateo Wilderness Area, "Miller Canyon" on the south base and flank of Miller Mtn from 8S02 upstream to the eastern summit area. T8S,R5W, sect. 10.15, 2100–2900', 3 Mar 1992, *Boyd & Ross 6717* (RSA); W. of Warner Hot Springs, 6 Apr 1929, *Clark 2007* (RSA); South side of Gonzales Canyon, east of Del Mar, 30 Mar 1969, *Copp 69-1* (CAS); Mt. Soledad, 3 Jan 1935, *Gander 103* (RSA, UC); North side of San Miguel Mountain. 32°42′N 116°55 3/4′W, 900', 24 April 1957, *Moran 6000* (DS); Beaumont, 2000', 25 Mar 1919, *Munz, Street & Williams 2327* (ORE); Colorado Desert, 1500', 9 Apr 1921, *Spencer 231* (POM); Potrero Grade, 18 Mar 1917, *Spencer s.n., 9 Apr. 1921* (POM); Grape Vine Canyon, 1200 m, 21 May 1930, *Templeton 1625* (RSA-2); Near Santee, Feb 1915, *Valentien s.n.* (UC). San Louis Obispo County: Atascadero, 22 Mar 1926, *Abrams 10942* (DS); 4.4 mi east of Santa Margarita; La Panza Range, 1200', 29 Mar 1962, *Breedlove 2029* (DS); 3 mi E. of Pozo, sect. 13, T.30S, R.15E, 1800', 27 Mar 1937, *Gifford 801* (UC); 1 mi S. of Bee Rock, Bradley, Sec 7, T.25S, R.10E, 1200', 11 Apr 1938, *Graham 305* (UC); 7X Ranch, Santa Lucia Mountains, 2200', 2 Mar 1956, 2200', *Hardman 143* (CAS); 7X Ranch, Santa Lucia Mountains, 2200', 2 Mar 1956, 2200', *Hardman 144* (CAS); Santa Rita Canyon, Santa Lucia Mountains, 13 Apr 1956, *Hardman 404* (CAS); L. Delagenna

Ranch, Santa Lucia Mountains, 26 Apr 1956, *Hardman 533* (CAS); Calf Canyon, 5 Apr 1967, *Hoover 10334* (CAS); E. side of Santa Margarita Lake, 8 Apr 1986, *Keil 19136* (RSA); 3 mi N. E. of Templeton, Paso Robles, T. 27S, R. 12E, 900', 31 Mar 1937, *Lee 806* (UC); Growing in a disturbed area on a road bank beside Hwy. #229, 5.9 mi. sw. of Hwy. #41 at Creston, 29 Mar 1981, *McNeal 2433* (OSC); Riconda Trail Head off Pozo Road. N 35°17.214, W 120°28.659′, 2200', 18 May 1998, *Monfils 2* (MSC); Riconda Trail Head off Pozo Road. N 35°17.267, W 120°28.677′, 2070', 27 May 1998, *Monfils 20*, (MSC); Santa Rita Canyon, 1000', 17 Apr 1957, *Sprague 1136* (RSA); On Cayucos Rd. to Cambira on Jack Mt. Nick Marquat Ranch, 16 Apr 1957, *Sprague 1137* (RSA); Hill by a spring near San Louis Obispo,May 1889, *Summers 527* (CAS); 2 mi north Cuesta Pass, Santa Lucia Mountains, 2000', 4 Apr 1963, *Toschi 63:97* (CAS); Santa Margarita, Eldorado School, 20 Apr 1933, *Wall s.n.* (CAS-2, RSA); Roadside and hills near Adelaide, W. of Paso Robles, 24 Mar 1932, *Wiggins 5847* (CAS, DS, POM); Prefumo Canyon, *no collector* (DS). San Mateo County: Woodside, 16 Mar 1902, *Abrams 2278* (DS); Kings Mountain Road, Santa Cruz Mountains, 500–700', 1 Mar 1914, *Abrams 5058* (POM); Woodside, 3 Mar 1895, *Applegate 421* (DS); Woods on Coal Mine Ridge, 23 May 1937, *Barry 155* (DS); Hill east of Lake Searsville, North Slope, 2 Mar 1929, *Benson 987* (POM); Woodside, Santa Cruz Mtns, near San Fransquito Cr., 600', 28 Feb 1931, *Benson 2610* (POM); Santa Cruz Mountain Peninsula, Crystal Spring Lake, 28 Apr 1920, *Borthwick 97* (DS); Near the intersection of Canada and Edgewood roads. About 3 mi. westward from Redwood City, 13 May 1974, *Cahill 248* (DS); La Honda Road (from Hwy. 5) to Woodside, 3 mi. from Mt. Home-Portola road, 4 Apr 1956, *Campbell 1* (RSA); Big Basin of Pescadero creek, 9 May 1903, *Copeland 3050* (POM); Santa Cruz Peninsula, near Belmont, no date, *Dudley s.n.* (DS); Woodside, 1903 May, *Elmer 4497* (CAS-2, DS, ORE, OSC, POM, UC); Near Belmont, Mar 1886, *Greene 9* (ORE); San Carlos, Chaparral area north of Malabar Rd. and Melendy Dr. Lat N. 37°29′38″, Long. 122°16′41″W, 600–680', 22 Apr 1973, *Hemphill 737* (DS); Woods near Spring Valley Lakes, Santa Cruz Mountain Peninsula, 29 Apr 1920, *Hickborn s.n.* (DS); Los Trancos, 30 Apr 1908, *Lewis s.n.* (RSA); Kings Mt., May 1902, *McMurphy s.n.* (DS); Mt. above Woodside, 9 Mar 1906, *McMurphy s.n.* (DS); Sawyer's Road, near Crystal Springs lake above Burlingame and Millbrae, 15 Apr 1956, *O'Bannon s.n.* (DS); Sawyer Ridge, 17 Apr 1949, *Oberlander 86* (DS); Santa Cruz Peninsula, Kings Mt., 27 Apr 1907, *Patterson s.n.* (RSA); Santa Cruz Peninsula, Kings Mt. Road, 27 Apr 1907, *Randall 394* (DS); Santa Cruz Peninsula, Kings Mt. Road, 28 Mar 1908, *Randall s.n.* (DS, RSA); Belmont, 24 Feb 1935, *Rose 35016* (RSA); Crystal Springs lake, 500', 12 Apr 1939, *Rose 39061* (RSA, UC); Millbrae Highlands, 300', 31 Mar 1948, *Rose 48031* (RSA); Emerald Lake, w. of Redwood City, 400', 23 Mar 1964, *Rose 64013* (DS, RSA); 2 mi. nw of Woodside, 600', 27 Mar 1969, *Rose 69009* (MSC); King's Mountain, 27 Apr 1907, *Rust 135* (RSA); King's Mountain Road, 29 Mar 1949, *Thomas 195* (DS); Jasper Ridge, about 5 mi southwest of Palo Alto. Lat N. 37°24.5′, Long. 122°14′ W, 500', 5 Apr 1959, *Thomas 7663* (MSC); ½ way up east slope of La Honda Grade, Santa Cruz Mts., 24 Jan 1927, *Wolf 190* (RSA); East side of La Honda Grade, 26 Feb 1927, *Wolf 221* (RSA); Above Searsville Lake, 2 Mar 1927, *Wolf 235* (RSA). Santa Barbara County: Purissima Hills, on road to Mission, 27 Mar 1938, *Abrams 13755*, (DS); North side of the Point Sal Ridge, 3 ½ mi. west of Corralillos Canyon. Point Sal, 3 Mar 1958, *Blakley & Muller B-2695* (CAS-2, RSA); Beside Refugio Pass Road, 5.4 mi north of U.S. 101, 24 Feb 1962, *Breedlove 1778* (DS); San Marcos Pass. Old Stagecoach Road. N 34°31.790′, W 119°50.070′, 1402', 17 May 1998, *Monfils 1* (MSC); Old Freemont Trail and Coach Rd., Santa Ynez Mts., Area of Refugio Pass, 2200', 18 Mar 1956, *Pollard s.n.* (CAS); Near summit of Refugio Pass, Santa Ynez Mts, 2200', 19 Apr 1968, *Pollard s.n.* (CAS); Stagecoach Road, 1650', 5 Apr 1970, *Shevock 106* (RSA); Entrance to Foster Glen Park, along highway in San Marcos Pass, south side of Santa Ynez Mountains near summit, 11 Mar 1955, *Smith 3918* (RSA, UC); Three miles north of summit of San Marcos Pass, 19 Mar 1961, *Turner, Sphon & Ball C-494* (RSA). Santa Clara County: Santa Cruz Peninsula, charcoal burners, Page Mill Road, Black Mt., 6 Jul 1903, *Dudley s.n.* (DS); Santa Cruz Peninsula, Page Mill Road, Black Mt., 23 Apr 1904, *Dudley s.n.* (DS); Adelante Villa, Palo Alto, 25 Feb 1894, *A. M. K. s.n.* (RSA); Foothills near Stanford University, 9 Mar and 15 May 1902, *Baker 283* (CAS, DS, MSC-2, POM, UC); Black Mt., 9 Feb 1895, *Burnham 9 Feb. 1895* (MSC); Eastern slope of Mount Hamilton, 3000', 31 Mar 1933, *Chambers 144* (UC); Los Gatos, 19 Mar 1897, *Davy s.n.* (UC); North-facing bank, south side of page Mill road, ca. 1 mi west of entrance to Palo Alto Foothills Park, Palo Alto, 1200', 25 Mar 1969, *Doty 593* (RSA); Foothills west of Los Gatos, 25 Mar 1904, *Heller 7281* (DS, MSC, UC); Alpine Creek Road, northeast side of Santa Cruz Mountains, 200', 22 Feb 1932, *Keck 1387* (DS, RSA); Foothills of the eastern side of the Santa Cruz Mountains, 5 mi south of the center of Palo Alto. Los Tracos Trail above Los Tracos Creek, 600–1800', 3 Apr 1974, *Martineau 16* (DS); 23.1 mi. w. of Interstate #5, Patterson exit, in Del Puerto canyon (2.5 mi. e. of the Mt. Hamilton-Livermore Rd.), 15 Mar 1970, *McNeal 472* (OSC); Fire trail near Loma base above spring, 3400', 21 Mar 1940, *Nelson 71* (UC); Hills 1 ½ miles south od Saratoga, Western Santa Clara County, 800', 1 Mar 1906, *Pendleton 290* (POM); 10 mi south of Black Mountain, s. of Palo Alto, 1200–1300', 16 May 1940, *Pennell & Abrams 25429* (CAS, UC); Seeboy Ridge, Mount Hamilton Range, 2400', 10 Feb 1934, *Sharsmith 537* (UC); South end of Mount Day Ridge above Santa Isabella Creek, Mount Hamilton Range, 1800', 25 Mar 1935, *Sharsmith 1520* (UC); Northwest slope of Black Mountain, 1100', 31 Jan 1948, *Silva 2616* (RSA); Vicinity of Mt. Umunhum, Lat. N. 37°09.5′, Long. 121°54.2′ W, 3400', 23 Apr 1954, *Thomas 3963* (DS). Santa Cruz County: Ben Lomond Mountain area; on Eagle Rock; T9S, R3W, sect. 16, 2200', 23 Mar 1974, *Halse 986* (OSC); Big Basin, Santa Cruz Mts., *Reed s.n.* (CAS); Santa Cruz Peninsula, Swanton, Spring 1912, *Rich s.n.* (DS); La Honda Rd. Sta. Cruz Mts., 2000', 3 Apr 1956, *Sprague 1095* (RSA); Between Eagle Rock and Locatelli Ranch. Lat. N. 37°08.7′, Long. 122°12′W, 2400', 27 Mar 1950, *Thomas 1346* (DS); East side of Mill Creek Drainage about 2 mi S-SW of Eagle Rock at Lat. N. 37°07.3′, Long. 122°12.4′W, 1800–1900', 30 Apr 1954, *Thomas 3035* (DS); Between Eagle Rock and Locatelli Ranch. Lat. N. 37°08.7′, Long. 122°12′W, 2200', 15 Mar 1954, *Thomas 3776* (DS); Vicinity of Eagle Rock. Lat N. 37

08.8, Long. 122 11.7 W. 2200–2500', 30 Mar 1961, *Thomas 9041* (DS); Halfway down La Honda Rd. Sta. Cruz Mts., 2000',13 Apr 1957, *no collector* (RSA); Solano County: Gates Canyon, northwest of Vacaville, 3 Mar 1951, *Kehlor s. n.* (OSC); 3 ½ miles west of Rockville, 25 Mar 1966, *Olson & Gorelick* (RSA-2). Sonoma County: Pepperwood Ranch, Oak woodland between the 2 fir-Redwood canyons, 25 Mar 1981, *Denevers 565* (CAS); Calistoga, 25 Mar 1922, *Eastwood 11097* (CAS); Camp Meeker, 22 Mar 1924, *Howell 287* (CAS); Near Sonoma, Mar 1962, *Menzius s.n.* (CAS); 2 mi from juncture of Highway 12 and Triniti Road, 750', 27 Feb 1960, *Ruckert 5* (CAS). Sonoma County, 10 Mar 1903, *Rattan s.n.* (DS); 0.5 mi. south of Calistoga, 400', 29 Mar 1953, *Raven 5207* (CAS); Santa Rosa Creek Canyon, 8–10 mi east of Santa Rosa, 25 Mar 1937, *Robbins 10* (UC); N. side of Vine Hill School Road ½ miles from Vine Hill Road, 250', 19 Apr 1965, *Thorne 34319* (RSA); Parker Hill Rd. ca. 2 ½ mi. N of Santa Rosa and 1 mi. N of Sonoma Co. Hosp., 350', 20 Apr 1965, *Thorne 34328* (RSA). Stanislaus County: Near head of Del Puerto Canyon, 20 Apr 1941, *Hoover 4886* (UC). Trinity County: Vic. Dam at Ruth Resevoir on Mad River, 2700', 21 May 1979, *Mattoon 121* (RSA, UC); Road along Coffee Creek, above Coffee Creek Ranch, 16 Jun 1956, *McClintock s. n.* (CAS); T6N, R6E, sect. 34, Found in Grays Falls Campground, 21 Apr 1979, *Miller 2-87* (RSA); sect. 10, T4S, R7E, West slope of Salt Cr., 2400', 28 May 1933, *Sack & Iverson 70393* (CAS); New River Trail from Grays Falls Campground on the North side of the Trinity River and west side of the New River, 800–1000', 7 Apr 1973, *Smith 6006* (RSA); Under scattered yellow pine; along Van Duzen River, about 3 mi southeast of Kuntz, 20 Apr 1950, *Tracy 18633* (RSA, UC). Ventura County: Las Turas Lake, Santa Monica Mts., 14 Feb 1931, *Ewan 4027* (POM); Upper Ojai, Ojai Valley and vicinity, 7 Mar 1895, *Pettibone & Hubby s.n.* (CAS); Hills north of Ojai, Upper Ojai, Ventura River Basin, 16 Apr 1949, *Pollard s. n.* (CAS); Hills north of Ojai, Upper Ojai, Ventura River Basin, 21 Apr 1949, *Pollard s. n.* (CAS), County Unknown: Belmont (MSC); California, 1853–1854, *Bigelow s.n.* (DS); S. Oakland Hills, Mar 1900, *Carruth s.n.* (CAS); Mt. Hamilton, 3000', 3 Apr 1906, *Chaualer 6014* (UC); Cuesta Summit, 2600', 2 Apr 1908, *Condit s.n.* (UC); California, *Coulter s.n.* (UC); Mt. St. Helena, 1 May 1918, *Eastwood 6811* (CAS, UC); Near Woodville, May 1889, *Howell 1387* (ORE); Northern California, 7 Apr 1937, *Javete s.n.* (OSC); Napa River Basin, Trail to beaux's Cabin, 25 Apr 1893, *Jepson s.n.* (UC); Near San Jaun Hot Springs, 6 Mar 1913, *Perkins s.n.* (RSA); Oakland, 1903, *Rattan s.n.* (DS); California, 1889, *Wright s.n.* (UC). MEXICO: **Baja California:** Elev. Of peak with microwave towers at 1275 m, 32°19′N–116°40′W, collections made from peak to base (ca. 600 m), *Thorne et al. 62130* (CAS, RSA).

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NOMENCLATURAL NOTES AND LECTOTYPES IN THE *ALLOCARYA* SECTION OF *PLAGIOBOTHRYS*

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ABSTRACT

The history of the combination *Plagiobothrys figuratus* (Piper) I. M. Johnst. ex M. Peck is explained, and *P. figuratus* var. *corallicarpus* (Piper) K. L. Chambers is proposed to replace an earlier combination at the subspecific rank. In the *Plagiobothrys scouleri* (Hook. & Arn.) I. M. Johnst. complex, the following are recognized as separate species for treatment in the Oregon Flora Checklist: *P. scouleri*, *P. reticulatus* (Piper) I. M. Johnst., *P. bracteatus* (Howell) I. M. Johnst., and *P. hispidulus* (Greene) I. M. Johnst.. *Plagiobothrys cusickii* (Greene) I. M. Johnst. is made a synonym of the latter taxon. Lectotypes are provided for *Allocarya bracteata* Howell, *A. cusickii* var. *vallicola* Jeps., *A. charaxata* var. *debilis* Brand, *A. commixta* Brand, and *A. piperi* Brand.

Key Words: *Allocarya*, Boraginaceae, lectotype, Oregon flora, *Plagiobothrys*.

While preparing the treatment of *Plagiobothrys* for the Oregon Flora Checklist, I encountered several nomenclatural anomalies involving *P. figuratus* and members of the *P. scouleri* complex. The following notes attempt to resolve these problems and to point out the need for further taxonomic study of these species. Because of the lack of useful biosystematic information on *Plagiobothrys*, I have employed a classical taxonomic approach, with principal emphasis on nutlet morphology of the included taxa.

PLAGIOBOTHRYS FIGURATUS

This taxon, Fig. 1A, is the common large-flowered *Plagiobothrys* species of western Oregon and adjacent Washington, whose range extends south to Curry County where the original type specimen was collected. The combination *P. figuratus* (Piper) I. M. Johnst. was published by Morton Peck (1941, p. 609), hence the authorities are usually cited as "I. M. Johnst. ex M. Peck." Neither in this first edition of his Manual nor in the second, posthumous edition (1961, p. 661) did Peck cite a basionym for his combination, the only synonym mentioned being "*Allocarya scouleri* Greene". Knowledge of pertinent prior literature is needed to trace the basionym, *Allocarya figurata* Piper (1920, p. 101). The rule requiring a clear indication of the name-bringing basionym, with place and date of publication, to validate a new combination of a previously published epithet dates only from January 1, 1953 (J. Lanjouw et al. 1952, p. 27). Hence, *Plagiobothrys figuratus*, as published by Peck, is a valid name. In his most recent paper on *Plagiobothrys* before 1941, Johnston (1935, p. 193) had treated *A. figurata* as a variety of *P. hirtus* (Greene) I. M. Johnst.. The reason that Peck, in 1941, attributed a new combination at the species rank to Johnston is probably a letter that Johnston had sent to him, dated October 3, 1939 (on file at Oregon State University), alluding to a Peck collection of *P. hirtus* with the following statement, quoted verbatim:

> These collections are very interesting. They clearly represent this poorly understood species. I now am inclined to believe that the common forms of the old Allocarya Scouleri aucts. should be separated from P. hirtus. If this is done, your plant of the Willamette Valley will have to be called Allocarya figuratus (sic!) Piper. You will recall that the type of Scouleri, which I examined at Kew, turned out to be different from the plant to which Gray applied the name.

Previously (Chambers 1989) I called attention to the fact that the southwestern Oregon taxon described by Piper as *Allocarya corallicarpa* (see Addenda), which Johnston had made a variety of *P. hirtus* (Johnston 1935, p. 193), is better recognized as a geographical race of *P. figuratus*. Although I selected the subspecific rank for this new combination, I now believe that varietal rank is more consistent with the infraspecific classifications used by other authors (e.g., Johnston 1932, 1935; Cronquist et al. 1984; Dorn 1988, p. 295; Messick 1993). A new combination is proposed in the Addenda.

THE *PLAGIOBOTHRYS SCOULERI* COMPLEX

As pointed out by T. C. Messick (1993), a number of taxa of *Plagiobothrys* that were recognized as species by I. M. Johnston (1932) appear to form an intergradent group usually referred to as the *P. scouleri* complex. This complex, discussed below, includes *P. bracteatus*,

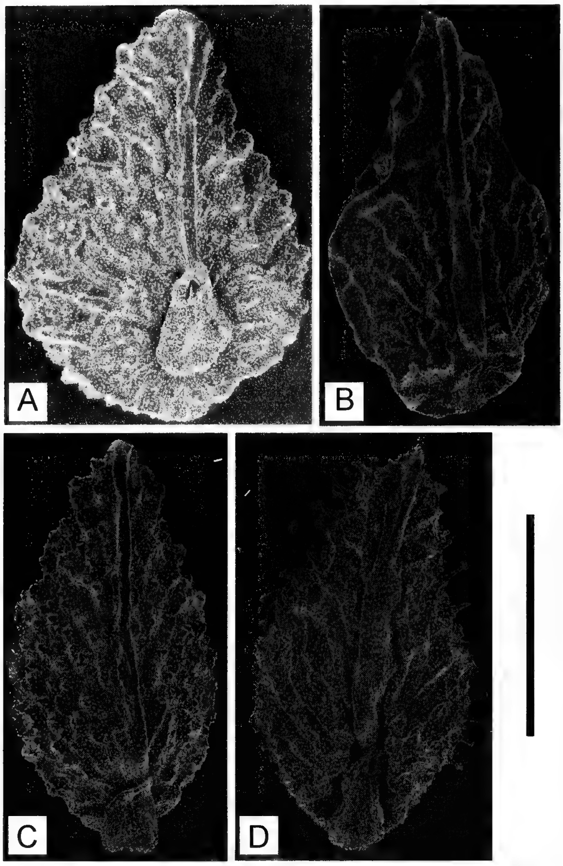

FIG. 1. Nutlets of some species of *Plagiobothrys* in Oregon. A. *P. figuratus* (Piper) I. M. Johnst. ex M. Peck var. *figuratus*. B. *P. bracteatus* (Howell) I. M. Johnst.. C. *P. scouleri* (Hook. & Arn.) I. M. Johnst.. D. *P. hispidulus* (Greene) I. M. Johnst.. Scale = 1 mm.

P. cognatus, *P. cusickii*, *P. hispidulus*, *P. reticulatus*, and *P. scouleri*. Johnston's treatment is repeated by Abrams (1951, pp. 557–571, as *Allocarya*) and Messick (1993, pp. 386–390, as *Plagiobothrys*). In the publications of Arthur Cronquist, however (Hitchcock et al. 1959, pp. 236–243; Cronquist et al. 1984, pp. 268–276), the second, third, and fourth names, above—as well as the more eastern taxon *P. scopulorum* (Greene) I. M. Johnst.—are made synonyms of *P. scouleri*, under the varietal epithet var. *penicillatus* (Greene) Cronquist. Dorn (1988) replaced this incorrect varietal name with the priorable autonym var. *hispidulus* Greene, which had been created when Jepson (1925, p. 853) published the combination *Allocarya hispidula* var. *penicillata*.

In the above group of taxa, *Plagiobothrys reticulatus* (Piper) I. M. Johnst. is a coastal species, ranging from the San Francisco Bay area to southwestern Oregon. Its defining trait is that the nutlet's attachment scar and part of the ventral keel lie in a trough formed by two parallel ridges of the pericarp. This taxon was first named *Myosotis californica* Fisch. & C. A. Mey. (Ind. Sem. Hort. Petrop. 2: 42. 1835), but that epithet cannot be used in *Plagiobothrys* because of the name *P. californicus* Greene, a synonym of *P. collinus* (Philbr.) I. M. Johnst.. Both *P. reticulatus* and *P. bracteatus* are outside the ranges covered in Cronquist's two publications (1959, 1984) and are therefore not mentioned in his treatment of *P. scouleri*. Depending on the degree of development of the nutlet's ventral trough, *P. reticulatus* may intergrade with more inland representatives of the *P. scouleri* complex through its var. *rossianorum* I. M. Johnst. (Johnston 1932, p. 71; Messick 1993).

The first listed taxon, *Plagiobothrys bracteatus* (Howell) I. M. Johnst., is recognized as a widespread taxon in the California Floristic Province, found more inland than *P. reticulatus* (Johnston 1932, pp. 68–71; Abrams 1951, p. 570; Messick 1993, p. 388). It was described by Thomas Howell as *Allocarya bracteata* (1901, pp. 281–282, not "J. Howell" of Messick 1993), mentioning no type but citing the locality: "In wet places, Umpqua Valley Oregon." Piper (1920, p. 113) placed the name in his list of doubtful species, stating: "There is no specimen in the Howell Herbarium marked *A. bracteata*...nor have any been seen elsewhere." Johnston (1932, p. 70) also wrote: "The type, unfortunately, appears to have been lost...What is more no isotype has been discovered." However, in the herbarium of Oregon State University is an authentic collection by Thomas Howell, which can be taken as the lectotype of *Allocarya bracteata* (see Addenda). Of the two plants on the lectotype sheet, the designated plant has better developed, though still immature, nutlets. The label is in Howell's handwriting and bears the name *Krynitzkia californica* Gray. This name, based on *Myosotis californica* Fisch. & C. A. Mey. (type from Fort Ross, Sonoma County), had been broadly used by Gray and others to apply to inland taxa including *P. bracteatus* (Jepson 1943, p. 364, see discussion in synonymy of *Allocarya cusickii* var. *vallicola* Jeps.).

Although limited in Oregon to the southwestern counties, up to the southern Willamette Valley, *Plagiobothrys bracteatus* appears to be widespread and well characterized in California, from the Central Valley and Sierra foothills south to San Diego County and northern Baja California. Its distinctive feature is the scar of the nutlets, which is consistently described as small, oblique-basal, ovate to elliptic or cuneate, and surrounded by an irregular ridge of pericarp tissue. A nutlet of this type, from the northernmost range of the species, is illustrated in Fig. 1B. The synonymy of this species includes four names that require lectotypification. The first of these is

Allocarya cusickii var. *vallicola* Jeps., mentioned above. Jepson's publication (1943, p. 364) cites no type collection, only giving a synonymy that includes the names *Krynitzkia californica* Gray "in greater part," *Allocarya californica* Greene "in great part, if not wholly, Great Valley plants," *A. bracteata* Howell, *A. commixta* Brand, and *A. piperi* Brand. A lectotype has been selected from the numerous collections mentioned by Jepson (see Addenda).

Jepson (1943, p. 364) also makes the combination *Allocarya cusickii* var. *debilis* (Brand) Jeps., based on *A. charaxata* var. *debilis* Brand, type: "Californien: Butte County: Chico (Copeland n. 3046, Herb. Berlin)." This and the other Brand holotypes mentioned here were lost in a fire during World War II (R. Vogt, Botanischer Garten und Botanisches Museum Berlin-Dahlem, personal communication). An isotype at UC has been selected as lectotype (see Addenda). I have examined this specimen and believe it represents no more than a growth form of *Plagiobothrys bracteatus*. Also requiring lectotypification are two other Brand names cited by Jepson, above, *A. commixta* and *A. piperi* (see Addenda).

Johnston (1935, p. 192) lectotypified *Myosotis scouleri* Hook. & Arn., the basionym of *Plagiobothrys scouleri* (Hook. & Arn.) I. M. Johnst., with a collection in the Hooker Herbarium at K labeled "N. W. Coast, Dr. Scouler." He hypothesized that Scouler's collection came from northwestern Washington or Vancouver Island, but it might equally well have been from along the Columbia River. Plants common in western Oregon, to which the name *P. scouleri* is being applied here, have nutlets of the type shown in Fig. 1C. The scar is prominent, not surrounded by a ridge of pericarp, and basi-lateral; that is, it is at the end of the nutlet but faces the lateral plane of the ventral surface. In practice, no sharp distinction can be drawn between this type of scar and the oblique-basal one of *P. bracteatus*, and in southwestern Oregon the assignment of specimens to one or the other species may be arbitrary. If *P. bracteatus* were to be reduced to varietal status under *P. scouleri*, the epithet *debilis* of Brand would appear to have priority. However, no such combination is proposed here.

A type of nutlet found very commonly in plants from east of the Cascades in Washington and Oregon, south principally in the Sierra Nevada to the mountains of southern California, is what I recognize as *Plagiobothrys hispidulus* (Greene) I. M. Johnston (Fig. 1D). The scar is near the base of the nutlet but is distinctly lateral (not oblique) in orientation and is usually enclosed in an areole formed by a surrounding ridge of the pericarp. The scar varies in shape, even on individual plants, but is mostly longer than wide, and is concave with spreading margins. Frequently, however, the scar appears cuneate or linear because the margins bend upward after release from the gynobase, an inconsistent feature that putatively defines the taxon *P. cusickii* (Greene) I. M. Johnst.. This and other minor differences in pericarp surface between *P. cusickii* and *P. hispidulus* are too variable to merit species distinction, in my opinion. Thus, I here combine these two entities taxonomically, choosing the epithet *hispidulus* (basionym *Allocarya hispidula* Greene, 1887, p. 17) over the simultaneously published *Allocarya cusickii* Greene.

To what extent the name *Plagiobothrys cognatus* (Greene) I. M. Johnst. (basionym *Allocarya cognata* Greene, 1901, pp. 235–6) applies to plants in the Pacific Coast states is uncertain and requires a more detailed and varied study than is possible from available herbarium specimens. The type came from Cache Valley, Utah. At present, I am not using this name in the Oregon Flora Checklist.

Addenda

Plagiobothrys figuratus (Piper) I. M. Johnst. ex M. Peck var. **corallicarpus** (Piper) K. L. Chambers, *stat. nov.* Based on *Allocarya corallicarpa* Piper, Proc. Biol. Soc. Wash. 37: 93–94. 1924. **Type**: Oregon, Josephine Co., Grants Pass. June 2, 1921. *C. V. Piper 5021* (holotype US!; isotypes, GH!, WS!).

Allocarya bracteata Howell, Fl. N. W. Amer. 1(5): 481–2. 1901. **Lectotype** here designated: Oregon, Umpqua Valley, April 1887, *Thomas Howell s.n.* (OSC 61550, the plant at the left).

Allocarya cusickii var. **vallicola** Jeps., Fl. Calif. 3(2): 364. 1943. **Lectotype** here designated: California, Napa Co., Napa Valley near Calistoga, May 2, 1897, *W. L. Jepson 21,170* (JEPS 60937, annotated with this name by Jepson).

Allocarya charaxata var. **debilis** Brand, Engler, Pflanzenr. 4(252), Heft 97: 165. 1931. Isotype here designated as **lectotype**: California, Butte Co., Chico, in dry ditch beds, May 15, 1903, *E. B. Copeland 3046*, in distribution by C. F. Baker (UC 75319, the plant in upper right corner; **isolectotype**: GH 93309)). These sheets are also **isotypes** of *Allocarya conjuncta* Piper, Contr. U.S. Natl. Herb. 22: 109. 1920, a nomenclatural synonym.

Allocarya commixta Brand, Repert. Spec. Nov. Regni Veg. 18: 312. 1922. Isotype here designated as **lectotype**: California, Santa Clara County, Park's Ranch, Mt. Hamilton Range, elevation 2700 ft, April 28, 1908, *A. A. Heller 8911* (GH 93308, the third plant from the right, middle row).

Allocarya piperi Brand, Repert. Spec. Nov. Regni Veg. 19: 70. 1923. Isotype here designated as **lectotype**: California, Napa County, near Napa, April 25, 1902, *A. A. Heller & H. E. Brown 5361* (GH 93605, the plant at the top).

Acknowledgments

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NOMENCLATURE OF THE SPURRED-GENTIAN OF THE SOUTHWESTERN UNITED STATES AND NORTHWESTERN MEXICO, *HALENIA ROTHROCKII* (GENTIANACEAE)

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ABSTRACT

The names *Swertia recurva* Sm. and *Halenia recurva* (Sm.) C.K. Allen are typified by a specimen of a species native to Colombia. The correct name for the western North American species that has been called *H. recurva* is *H. rothrockii* A. Gray.

RESUMEN

Se typifican los nombres *Swertia recurva* Sm. y *Halenia recurva* (Sm.) C.K. Allen por un espécimen de una especie indígena de Colombia. La especie de Norteamérica occidental la que ha se llamado *H. recurva* correctamente se llama *H. rothrockii* A. Gray.

Key Words: Arizona, Gentianaceae, *Halenia*, Mexico, New Mexico, nomenclature, taxonomy.

The southwestern spurred-gentian, formerly known as *Halenia rothrockii* A. Gray but since 1933 generally called *H. recurva* (Sm.) C.K. Allen, reaches the northern limits of its range in Arizona and New Mexico and is more widely distributed in the Mexican states of Chihuahua, Coahuila, Durango, and Sonora. The results of a study of the nomenclature of this species, the need for which became evident during research for the treatment of the Gentianaceae for the *Flora of North America North of Mexico*, are presented here.

Following its publication by J. E. Smith in 1816, the name *Swertia recurva* was for many years considered to be of uncertain applicability. Grisebach (1845) suggested that it might be synonymous with *Halenia gracilis* (H. B. K.) Griseb., a name correctly applied to a species native to Colombia and Ecuador, but he did not adopt the earlier epithet *recurva* for that species. Neither the name *S. recurva* nor any homotypic synonym thereof was accepted for any species until 1933, when Allen applied the new combination *Halenia recurva* (Sm.) C. K. Allen to the species of the southwestern United States and northwestern México that until then had been known as *H. rothrockii* A. Gray.

Smith (1816) based the name *Swertia recurva* on a specimen in the Linnaean herbarium, now designated LINN no. 327.6. As Smith cited no other specimens or literature, this specimen has consistently been accepted as the type, by authors including Allen (1933) and Wilbur (1984). It is labelled "*Swertiae corniculatae affinis*" in the lower left; "*Swertia recurva* Sm. in Rees's Cyclop." in the lower right; and "Escallon" in the upper right. In the original description of *S. recurva*, Smith (1816) said that it had been "Collected in Mexico by Escallon, and sent to Linnaeus by Mutis." Its presence in Linnaeus's herbarium, which Smith had acquired in 1784, was thus attributed to José Celestino Bruno Mutis y Bosio, who is known to have sent Colombian (but not Mexican) specimens to Linnaeus. Antonio Escallón y Flórez was one of Mutis's students and botanical associates in Colombia. Much has been recorded of Mutis's career, and it is quite certain that he never collected specimens in Mexico. Less is known about Escallón, but there is no indication of his having been in Mexico.

A specimen at US designated "type collection," i.e., considered to be an isotype, was acquired in 1932 in a set of Mutis's specimens from MA. It bears a printed label with the heading "Plants of Colombia collected by José Celestino Mutis, 1760–1808," and the handwritten identification "*Halenia recurva* (Smith) Allen." At the bottom of the label is the printed subheading "Mutis' notes accompanying specimens at Madrid," followed by the handwritten transcription "*Swertia corniculata*."

The history of these specimens is paralleled by that of the types of some other names based on Mutis's collections from Colombia now at LINN with isotypes at US. The species now known as *Otholobium mexicanum* (L.f.) J. W. Grimes, which does not occur in Mexico, was given the name *Indigofera mexicana* by Linné filius (1782) although he gave its range as "Nova Grenada" [=Colombia, sometimes also including Ecuador and Venezuela]. Both Linné filius and Smith (1791) gave the range of *Atractylis mexicana* L.f. [*Lycoseris mexicana* (L.f.) Cass.] as "Mexico,"

although, according to John Pruski (note in w^{3}TROPICOS, Missouri Botanical Garden Web site, 2004), the species is endemic to Colombia. Pruski gave the provenance of the type as Colombia and deemed "Habitat in Mexico" to be a "locality error by L.f." It appears that Linné filius applied the name "Mexico" to all or much of what was in his time mainland Spanish America, and that he was uncritically followed by Smith with regard to the provenance of specimens received from Mutis.

Smith's (1816) use of the term "Mexico," interpreted by later authors as denoting present-day Mexico, has been accorded primacy over all other evidence as to the provenance, and hence the identity, of the type of the name *Swertia recurva*. Shortly after Allen (1933) published her monograph, Ellsworth P. Killip pointed out that she had erred in citing Mutis as the collector of a specimen from Mexico (correspondence attached to isotype sheet at US). In her response (also attached to isotype sheet at US) she said that the specimen at US "may very well be part of the same collection, and hence from Mexico, not Colombia," quoting Smith as to the provenance of the holotype. Wilbur (1984) followed Allen in accepting Smith's statement that Escallón had collected the type in Mexico and given it to Mutis. He annotated the isotype at US "*Halenia recurva* (Sm.) C. K. Allen (*H. rothrockii* A. Gray)." K.B. von Hagen (annotations 2002, GH, MICH, NY, US) likewise accepted this premise and identified specimens from North America, including the holotype and isotypes of the name *H. rothrockii*, as *H. recurva*.

In view of the evidence that "Mexico" was incorrectly associated by Smith with specimens collected by Mutis in Colombia, it is appropriate to reconsider the identity and probable provenance of the type specimen of the name *Swertia recurva* independently of any a priori assumption that it must be of Mexican origin.

The *Halenia* species in northwestern Mexico and the southwestern United States, which I shall call *H. rothrockii* in the remainder of this discussion, differs from most other *Halenia* species in its widely divergent corolla spurs, which are slender, proximally horizontal and distally curved upward. However, in Colombia, where Mutis and Escallón botanized, there is another species with similarly slender, widely divergent spurs, *H. asclepiadea* (H. B. K.) G. Don (nomenclature and types discussed below). The name *Halenia cuatrecasasii* C. K. Allen is here considered to be a heterotypic synonym of *H. asclepiadea*. The type of that name (Colombia: Cundinamarca: Páramo de Chococontá, 2760–2830 m, *Cuatrecasas 9657*; holotype F, isotype NY) is likewise from Depto. Cundinamarca, Colombia, and the spurs are similar in shape and orientation to those of *H. asclepiadea*.

The Colombian *H. asclepiadea* and the North American *H. rothrockii* differ distinctly in growth form. *Halenia asclepiadea* is a rhizomatous perennial that usually produces several flowering stems in a cluster, sometimes accompanied by vegetative rosettes or stolon-like stems not flowering in the same season. This habit is evident in the holotype of the name *S. asclepiadea* at P-Bonpl. (Colombia: Cundinamarca: Juxta Santa Fé de Bogota, 1400–1700 hex., *Humboldt & Bonpland s.n.*), the isotype at US, and the isotype formerly at B, now represented by a photograph at F, as well as in more recent specimens. *Halenia rothrockii*, in contrast, is monocarpic, generally single-stemmed, with a slender tap root, as is well shown in the type collection cited below. The basal parts of the holotype of the name *S. recurva* at LINN indicate that the specimen is that of a perennial in which stolon-like non-flowering stems accompany the stems that are in flower. This specimen includes a stolon-like stem highly similar to one on the isotype of the name *H. cuatrecasasii*. The isotype at US also clearly represents a several-stemmed perennial, distinctly unlike *H. rothrockii* in habit and basal parts.

Halenia asclepiadea and *H. rothrockii* also differ in the shape of their floral parts. The calyx lobes of *H. asclepiadea* are triangular, tapering evenly from the base to the simply acute apex. Those of *H. rothrockii* are narrowly oblong with the sides parallel for much of their length, tapering rather abruptly in the distal one-third or less to a short-acuminate apex. The corolla lobes of *H. asclepiadea* remain wide for most of their length and are rather abruptly rounded to a strongly erose distal portion and a subacute apex, whereas those of *H. rothrockii* taper more gradually from near mid-length to an acuminate apex and have less prominently erose margins. Relatively wide-based, triangular calyx lobes characteristic of *H. asclepiadea*, and unlike those of *H. rothrockii*, are discernible in both the holotype and the isotype of the name *S. recurva*. The distal portions of the corolla lobes are not well spread out, but enough is visible of at least one corolla lobe of the holotype to support the identity of the specimen as *H. asclepiadea*.

Some published descriptions of the spurs of *H. asclepiadea* appear to be inconsistent with the appearance of the specimens studied by the respective authors. Gilg (1916) described the spurs of *H. asclepiadea* as "crassiuscula" and "dicken," and Allen (1933), in a key that closely followed Gilg's, described them as "thick." Of the three replicates of the type collection, the best-prepared specimen was the isotype at B, of which the extant photograph clearly shows flowers with relatively slender spurs similar to those of the type of the name *S. recurva*. The isotype at US, although of poorer quality, likewise shows slender spurs. The image of the holotype at P is

less clear in this respect, because of the condition of the specimen and the paper on which it is mounted and the excessive contrast in the microfiche, but it appears to represent the same species. It may be noted, moreover, that Allen (*in* Cuatrecasas 1942) described the spurs not only of *H. asclepiadea* but also of *H. cuatrecasasii* as thick, although those of the holotype and isotype specimens of the latter name likewise appear relatively slender.

Discrepancies in descriptions of the spurs of *H. asclepiadea* may be due in part to the apparent presence, pending further study, of two species of *Halenia* in Colombia with strongly divergent spurs, both of which have been identified as *H. asclepiadea*. The spurs of the plants called *H. asclepiadea* in this paper are ca. 1.5 mm in diameter near the base, proximally tapering abruptly but scarcely tapering otherwise. Those of other plants are relatively stout, ca. 2.5 mm in diameter at the base and tapering throughout their length, reminiscent in their shape, although not in their orientation, of the spurs of *Dicentra cucullaria* (L.) Bernh. This probably distinct species is well represented by *Uribe Uribe 5614* (F; image in "Neotropical Herbarium Specimens," Field Museum of Natural History Web site). The type collection of the name *S. recurva* is equated here with the first of these two entities.

From the evidence presented above, I conclude that the type of the name *Swertia recurva* Sm. represents the Colombian species now generally known as *Halenia asclepiadea*, and that the name *H. rothrockii* should be restored for the species in the southwestern United States and northwestern México.

Halenia rothrockii A. Gray, Proc. Amer. Acad. Arts 11: 84. 1876.–*Tetragonanthus rothrockii* (A.Gray) A. A. Heller, Cat. N. Amer. Pl., ed. 1, p. 6. 1898. Type: USA, Arizona, Graham Co., Mount Graham, 9000 ft, Aug 1874, *Rothrock 733* [number lacking on some isotypes] (holotype GH!; isotypes F, ISC, MO!, NY [image on Internet!], PH [microfiche!], US [image on Internet!])

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EREMOGONE CLIFTONII (CARYOPHYLLACEAE), A NEW SPECIES FROM CALIFORNIA

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ABSTRACT

Eremogone cliftonii is described as new from northern California. Petal and capsule lengths and presence or not of pubescence or a bloom on vegetative structures are features useful in distinguishing this novelty from *E. aculeata* and *E. kingii* var. *glabrescens*, the congeners found in the region. *Eremogone cliftonii* occurs in open or forested areas on decomposing granite.

Key Words: *Arenaria*, California, Caryophyllaceae, *Eremogone*, North America, Sierra Nevada.

Eremogone is a genus of about 90 species (Hartman and Rabeler 2004; Hartman et al. 2005) known from north-temperate regions from western Europe through Asia and western North America. Fifteen species including this novelty, and numerous varieties, are known in western North America. *Eremogone* plants are woody based, cespitose or matted, perennials with subulate to filiform leaves, erect or ascending flowering stems, and open to congested or umbellate cymes. Although often treated as a subgenus of *Arenaria* (e.g., McNeill 1962), molecular data support *Eremogone* as monophyletic and distinct from *Arenaria* (Nepokroeff et al. 2001)

Eremogone cliftonii Rabeler & R. L. Hartman, sp. nov. —TYPE: USA, California, Plumas Co., in roadside borrow pit, N side of CA 70, 0.5 km E of Chambers Creek, T24N R6E Sec. 3, SE ¼ of SE ¼, 39°57′29″N, 121°17′19″W, 622 m elevation. 20 Apr 2005, *R. K. Rabeler 1473 & L. P. Janeway, L. Hanson, L. Ahart* (Holotype: MICH; isotypes RM, UC). Fig. 1

Eremogone cliftonii, sp. nov. Herba perennis e caudicem ramis horizontalibus ad ascendentibus. Caules ascendens ad erecti, glabri. Folia filiformia ad aciformia, ascendentia ad arcuati-reflexa, marginibus proximale ciliolatibus, apice spinosa. Flores perfecti, regulares, saepe 9–25 in cyma patula; sepala ovata ad obovata, marginibus anguste vel late scariosis, apice plerumque obtusa ad rotundata vel late acuta, saepe apiculata; petala 5, alba, 12–18 mm longa, late patentia, sepalis 2.3–3.7-plo longiora, apice rotundata; antherae 10, vinaceae; styli 3, stigmatibus breve linearibus ad subcapitatis. Capsulae cylindrico-urceolatae, 7.5–9 mm longae, primitus dentibus 6 dehiscentes. Semina 5–9, nigra, pyriformi-compressa incisura hylari, tuberculata tuberculis humilibus rotundatis saepe elongatis.

Perennial herb (11)15–35 cm tall arising from a branched woody caudex with horizontal to ascending, often subterranean branches 5–15+ cm long; *Stems* simple or branched, ascending to erect, glabrous, rounded, internodes 0.5–5 mm long; *Leaves* opposite, exstipulate, with dense tufts of closely overlapping leaves at base of fertile stem and on sterile branchlets that are commonly present, cauline leaves more widely spaced, in 2–5 pairs on the main stem, gradually reduced above, filiform to commonly needle-like, mostly 2–6 cm long, 0.7–1.1 mm wide, ascending to widely spreading or arcuate-reflexed, flexuous, often adaxially grooved, especially proximally, the margins ciliolate proximally, the apex spinose; *Inflorescence* a (3) 9–25+ flowered, open cyme; *Pedicels* (5) 10–25 mm, stipitate-glandular; *Flowers* perfect, chasmogamous, regular; *Sepals* ovate, often broadly so (to obovate in inner series), 4.5–5.5 (6.5) mm long, lengthening up to 1 mm in fruit, lustrous, somewhat leathery, glabrous, margins narrowly or broadly scarious (especially inner series, to 0.8 mm wide), 1–3 veined, the lateral veins shorter and less developed, base somewhat thickened, apex usually obtuse to rounded (especially inner series) or broadly acute, often apiculate; *Petals* 5, white, oblong to elliptic, oblanceolate, or obovate, 12–18 mm long, widely spreading, 2.3–3.7 times the length of the sepals, apex rounded; *Anthers* 10, red-violet; *Nectaries* as a lateral and abaxial thickened, crescent-shaped, transverse band with

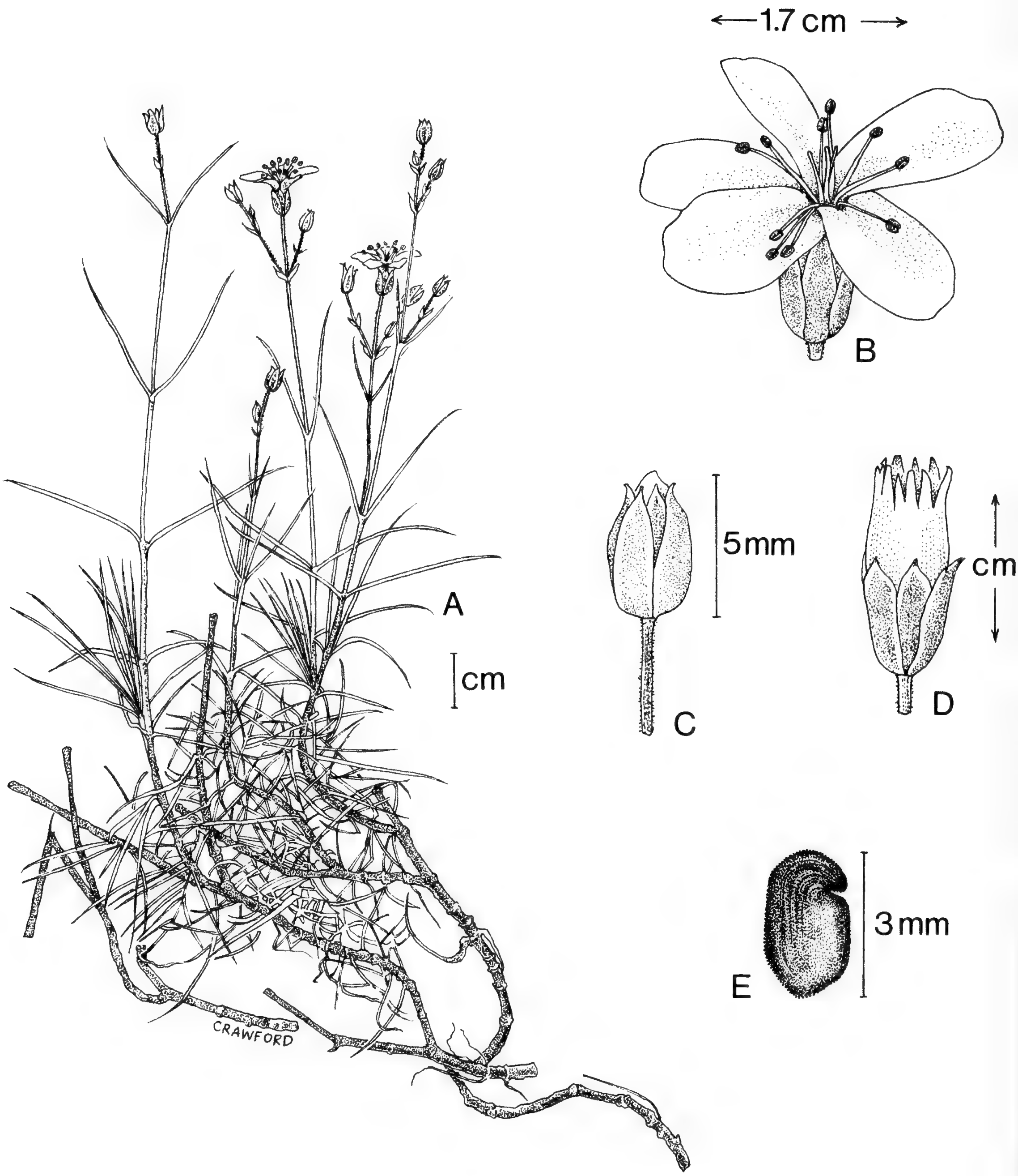

FIG. 1. *Eremogone cliftonii*. A. Habit. B. Flower. C. Bud. D. Dehisced fruit from previous year with subtending sepals. E. Seed. (From *Rabeler 1473*, MICH)

distal groove at the base of the antisepalous filaments, 0.5–0.6 mm long; *Ovary* 3-carpellate; ovules 5–11; styles 3, distinct, 8–10 mm long; stigmas short-linear to subcapitate; *Capsule* cylindric-urceolate, 7.5–9 mm long, glabrous, initially opening by 6 teeth dehiscing along the barely discernable sutures, each tooth then splits about half its length; irregular splitting may occur over time; *Seeds* 5–9, black, 2–3 mm long, pyriform-compressed with a hilar notch, tuberculate throughout, the tubercles low, rounded, short abaxially, elongate on the faces.

The paratypes cited below include all other collections we have examined. Habitat information suggests *E. cliftonii* to be a plant of open (often on slopes of roadcuts) or forested areas on decomposing granite at 455–1770 m elevation. The associated open forest is often a mixture of

ponderosa pine (*Pinus ponderosa* Dougl. ex Lawson & C. Lawson), sugar pine (*Pinus lambertiana* Dougl.), and white fir (*Abies concolor* (Gordon & Glend.) Hildebr.), along with manzanita (*Arctostaphylos* sp.), California black oak (*Quercus kelloggii* Newb.) and canyon live oak (*Quercus chrysolepis* Lieb.). The thirty-one known localities are in an area of about 1467 km^2 (567 mi^2) in Butte and Plumas counties; all are in the Feather River drainage within the Northern High Sierra Nevada subregion of the California Floristic Province (Hickman 1993). Although the geographical range is small, the plants are sometimes abundant; one label noted "about 400 plants" (*Hillaire 1216*), while another noted "about 800 plants" (*Hillaire 1225*).

Eremogone cliftonii is named for Glenn Clifton who, as part of his extensive collections towards a flora of Plumas County and the Plumas National Forest (Clifton 2003), recognized *E. cliftonii* as new (proposing the name "Arenaria grandiflora" without a Latin diagnosis, which would be a later homonym of *A. grandiflora* L., a European species). Apparently it was first collected in 1915 by A. A. Heller, then infrequently by several botanists until the 1980s when affiliates of the Chico State University herbarium documented it several times. Michael Baad apparently did not encounter it while doing field work for his dissertation on *Arenaria* subg. *Eremogone* (Baad 1969). Our first encounter with *E. cliftonii* was during preparation of the treatment of *Eremogone* for Flora of North America (Hartman et al. 2005). Barbara Ertter (UC) had sent Hartman several inflorescences of a plant gathered in the Feather River Canyon that she had been given to identify for use in a display at a flower show in Oakland, California. After seeing the large flowers, we immediately judged it unique not only among California material, but a new taxon, thus additional field and herbarium exploration was warranted. Lawrence Janeway (CHSC) and Linnea Hanson (U.S. Forest Service) were contacted. This led to surveys on the Plumas National Forest during 2005 and 2006 and the gathering of over one-third of the collections cited.

Most collections of *Eremogone cliftonii* that had been named were identified as *A. aculeata* S. Wats. (*E. aculeata* (S. Wats.) Ikonn.), *Arenaria macradenia* S. Watson subsp. *ferrisiae* Abrams (*E. ferrisiae* (Abrams) R. L. Hartm. & Rabeler), or simply identified to genus. Apparently selected specimens of *Heller 12071* (NY, UC, with few flowers with shriveled petals, mostly fruit; WTU, in late fruit) was the only collection seen by Baad. He annotated it as *A. aculeata*, as did Hartman while preparing a treatment for the Jepson Manual (UC only; Hartman 1993). Likewise, Hickman appears to have encountered the novelty but once during his study of *Arenaria* sect. *Eremogone* (Hickman 1971). He annotated *Balls & Lenz 20700* (DS, in full flower) as "a unique individual: seems to have some characters of *Arenaria pumicola californica* and *Arenaria macradenia*." Study subsequent to our FNA work has revealed that *Arenaria pumicola* Coville & Leiburg *var. californica* Maguire is more appropriately considered a synonym of *E. kingii* var. *glabrescens* (S. Watson) Dorn; *A. macradenia* would refer to material we now segregate as *E. ferrisiae* (Hartman et al. 2005). In comparing *E. ferrisiae* with *E. cliftonii* (character states of the latter in parentheses): sepals acute to acuminate, sometimes +− spine-tipped (generally obtuse to rounded or broadly acute, sometimes abruptly pointed), 3–4.3 (4.5–6.5) mm long, to 5.5 (7.5) mm long in fruit; petals 6–9 (12–18) mm long, and nectary glands 0.3–0.4 (0.5–0.6) mm long). Furthermore, *E. ferrisiae* is restricted to Mono, Inyo, and Tulare counties and a few sites further south in California. While both *E. aculeata* and *E. cliftonii* can be found in the northern Sierra, along with the frequently encountered *E. kingii* var. *glabrescens*, they can be distinguished as follows:

KEY TO *EREMOGONE CLIFTONII* AND CONGENERS IN THE REGION

1. Sepals generally obtuse to rounded or broadly acute, sometimes abruptly pointed
   2. Petals 4.5–10 mm long, ca. 1.2–1.3 times sepal length; stems glandular-hairy; leaves usually glaucous; capsules 5–7 mm long. . . . . *E. aculeata*
   2. Petals 12–18 mm long, 2.3–3.7 times sepals length; stems glabrous; leaves not glaucous; capsules 7.5–9 mm long . . . . *E. cliftonii*
1. Sepals acute to acuminate, sometimes ± spine-tipped . . . .*E. kingii* var. *glabrescens*

Paratypes. USA, California, **Butte County**: T25N R5E Sec. 21, 5000 ft. elev., 30 Jun 1962, *F. V. Brunett 110* (MICH); ca. 2 km SW of intersection of North Fork, Feather River and Plumas Co., T23N R5E Sec. 11, 490 m elev., 22 Jun 1977, *J. P. Warner 1* (CHSC); North Fork Feather River, 1.3 mi NE of Poe Power Dam, T23N R5E Sec 28, 1840 ft elev., 12 May 1980, *R. Banchero & R. A. Schlising 3588* (CHSC); 2.5 mi SE of Mountain House, [T22N R6E Sec. 33], 1100 m elev., 29 May 1980, *L. Ahart* 2362 (CHSC, DAV); ca. 3 mi NE of Milsap Bar, [T22N R7E Sec. 31], 1100 m elev., 10 Sep 1980, *L. Ahart 2636* (CHSC); S end of Walker Plains, T22N R6E Sec. 4, 5040 ft elev., 11 Jul 1980, *R. Schlising 3882* (CHSC); ca. 0.5 mi N of Mayaro, T23N R5E Sec. 21, 2000 ft elev., 21 May 1981, *M. S. Taylor 3793* (CAS [2], MO); 0.5 mi N of Ramsey Bar on Little Kimshew Creek, T24N R5E Sec. 20, 4650 ft elev., 29 Jun 1981, *R. Banchero & R. A. Schlising 4124* (CHSC); 0.8 mi SW of Ramsey Bar on Little Kimshew Creek,

T24N R5E Sec. 29, 4800 ft elev., 29 Jun 1981, *R. Banchero & R. Schlising* 4125 (CHSC); N end Concow area N of Flea Mt., T23N R5E Sec. 19, 3650 ft elev., 23 Jun 1982, *R. E. Preston, R. Banchero, & R. A. Schlising 4300* (CHSC); 2 mi E of Milsap Bar, T22N R7E Sec. 31, 900 m elev., 29 Jul 1983, *L. Ahart 4246* (CHSC, MICH, MO); along long sharp switchback in county rd 66553, T23N R5E Sec. 21, 2500 ft elev., 10 Sep 1984, *L.P. Janeway s.n. & R. Harrison, G. Benson* (CHSC); Feather River SE of Mayaro, T23N R5E Sec. 28, 1500 ft elev., 21 Apr 1985, *V. Oswald 1713* (CHSC); above hwy. 70, 3.1 mi NE of Pulga bridge, T23N R5E Sec. 28, 1559 ft elev., 20 May 1987, *L. P. Janeway 2082* (CHSC); side road (23N12Y) 0.6 mi from Four Trees Road, T23N R6E Sec. 32, 4800 ft elev., 28 May 1987, *L. P. Janeway 2111* (CHSC); 2.5 mi E of Granite Ridge along road to Lynch and Logue Meadows, T24N R5E Sec. 32, 4480 ft elev., 26 Jun 1987, *L. P. Janeway* 2307 (CHSC); along Concow Road, 3.6 mi N of Rag Dump, T24N R5E Sec. 31, 4500 ft elev., 20 Jun 1994, *L. P. Janeway 4669* (CHSC, RSA); Hwy 70, south side of canyon of North Fork Feather River, T23N R5E Sec. 27, 455 m elev., 28 May 2000, *L. P. Janeway & B. Castro 6745* (CHSC); 100 m W of the western driveway to Cresta Powerhouse, T23N R5E Sec. 27, 455 m elev., 20 Apr 2005, *R.K. Rabeler 1472 & L. P. Janeway, L. Hanson, L. Ahart* (CAS, GH, MICH, RM); 29 Jun 2005, *L. P. Janeway 8444 & L. Hanson* (CHSC, MICH); 3 Aug 2006, *R.K. Rabeler 1479 & J.A. Macklin* (GH, MICH, RM); along Pulga road on SW side of Dogwood Creek, T23N R5E Sec. 29, 594 m, 4 May 2005, *L. P. Janeway 8376 & M. Brown, S. Hillaire, J. Tuitele-Lewis* (CHSC); Pulga Road ca. 1.2 km E of Camp Creek, T23N R5E Sec. 21, 747 m elev., 4 May 2005, *L. P. Janeway 8377 & S. Hillaire, M. Brown, J. Tuitele-Lewis* (CHSC); just above Road 23N02, 0.2 km N of county road 66553, T23N R5E Sec. 20, 1073 m elev., 4 May 2005; *L. P. Janeway 8378 & M. Brown, S. Hillaire, J. Tuitele-Lewis* (CHSC); N of Pulga/Mayaro area, T23N R5E Sec. 20, 3340 ft elev., 4 May 2005, *S.M. Hillaire 1216 & M. Brown, L. P. Janeway, J. Lewis* (CHSC, RM); 0.7 km E of Lockerman Creek and 1.2 km ENE of its confluence at Camp Creek, T23N R5E Sec. 9, 1234 m elev., 11 May 2005, *L. P. Janeway 8388 & C. Christofferson, S. Hillaire, M. Brown, J. Tuitele-Lewis* (CHSC); 1.3 km NE of Flea Mountain, T23N R5E Sec. 19, 1152 m elev., 25 May 2005, *L. P. Janeway 8396 & M. Brown, J. Tuitele-Lewis* (CHSC); top of S end of Granite Ridge, about 2.3 km S of Kimshew Point, T23N R5E Sec. 6, 1317 m elev., 29 May 2005, *L. P. Janeway 8404* (CHSC, MICH); 0.2 km NW of Concow Road at the gap between the head of Rock Creek and the Little Kimshew Creek drainage, T24N R5E Sec. 29, 1478 m elev., 29 May 2005, *L. P. Janeway 8410* (CHSC, MICH); along road 22N62, S of Middle Fork Feather River, T22N R7E Sec. 31, 3120 ft elev.,10 Jun 2005, *S.M. Hillaire 1217 & M. Brown* (CHSC, RM); 2820 ft elev.,10 Jun 2005, *S.M. Hillaire 1218 & M. Brown* (CHSC); near Four Trees Road, T23N R6E Sec. 33, 4780 ft elev.,20 Jun 2005, *S.M. Hillaire 1224 & M. Brown* (CHSC, RM); N of Pulga, near Lockermans Creek, [T23N R5E Sec. 9], 3700 ft elev.,21 Jun 2005, *S.M. Hillaire 1223 & B. Castro* (CHSC, RM); 0.3 km W of Cedar Creek and 2.6 km NNW of mouth of Cedar Creek at North Fork Feather River, T23N R5E Sec. 9, 1295 m elev., 26 Jun 2005, *L. P. Janeway 8436* (CHSC, MICH);

Plumas County: Soapstone Ridge (Hill), 12 mi W of Bucks [Lake], [T23N R6E, Sec 15], 5500 ft elev., 7 Jul 1915, *A.A. Heller 12071* (BKL, CAS, DS, F, NY, UC, US, WTU); Camp Rogers [T24N R6E Sec 2], 2800 ft elev., 6 Jun 1920, *A. Head s.n.* (CAS); U.S. Hwy. 40 alt. (CA Hwy. 70), between Tobin and Camp Rogers, 13 May 1955, *E.K. Balls & L.W. Lenz 20700* (DS, RSA); Rodgers Flat, [T24N R6E Sec 2], 1967, *L. Rose 69075* (CAS); near Rogers Flat bridge, [T24N R6E Sec 2], 2000 ft elev, 23 Jun 1967, *J T. Howell 42741* (CAS, MICH, MO); near mouth of Chambers Creek [T24N R6E S3], ca. 2000 ft elev, 9 May 1967, *J.T. Howell & G.H. True 42224* (CAS); "Buck's Lake", T24N R6E Sec. 25 [TRS is west of Bucks Lake], 8 Jul 1975, *F. T. Griggs 120 & A. Pass* (CHSC); 9 Jul 1975, *D. Brink & L. Mayer s.n.* (CHSC); T24N R6E Sec 25, 12 Jul 1975, *F.T. Griggs & A. Pass 172* (CHSC); between Storrie and Belden, ca 2000 ft elev, 18 May 1976, G.L. Smith *s.n.* (CAS); between Indian Joe and Caribou [probably near Injun Jim Campground; T24N R6E Sec 9–10], 2000 ft elev, 17 Apr 1978, *C.B. Hardham 21583* (CAS, RSA); E side of Oroville-Quincy hwy at Walker Plains, T23N R6E Sec. 33, 5000 ft elev.,14 May 1981, *M. S. Taylor 3723* (MO); about 1.5 mi W of Sawmill Flat, T23N R9E Sec. 33, 5800 ft elev., 25 Jul 1986, *L. Ahart 5378* (CHSC); ca. 0.5 mi W of Little Marble Cone, T22N R7E Sec. 19, 30, 4800 ft elev., 3 Jul 1995, *B. Castro 579* (CHSC); sandy cut, Hwy 70, 2160 ft. elev., 26 Apr 1996, G. Clifton 34250 (G. Clifton herb); along hwy. 70, 0.5 mi E of Chambers Creek [T24N R6E Sec. 3], [622 m elev,], 9 Apr 1997, *D. W. Taylor 15947* (JEPS, UC); 17 Apr 1997, *G. Clifton 35331* (G. Clifton herb, not seen [cited *in* Clifton 2003]); 29 Jun 2005 *L.P. Janeway 8445 & L. Hanson* (CHSC, MICH); 3 Aug 2006, *R.K. Rabeler 1478 & J.A. Macklin* (CAS, GH, MICH, RM, RSA); near Lower Buck's Lake, T24N R6E Sec. 26, 5000 ft elev., 20 Jun 2005, *S.M. Hillaire 1225 & M. Brown* (CHSC, RM); above road 24N36, near Lower Buck's Lake, T24N R6E Sec. 26, 5000 ft elev., 20 Jun 2005, *S.M. Hillaire 1226 & M. Brown* (CHSC, RM); above road 24N04,

0.3 km S of crossing of North Valley Creek, T24N R5E, Sec. 23, 1347 m elev., 26 Jun 2005, *L. P. Janeway 8441* (CHSC, MICH); 4 Sep 2005, *L. P. Janeway 8536* (CHSC, MICH).

Acknowledgments

We thank David J. Keil for providing the Latin description; Barbara Ertter (UC) for bringing this novelty to our attention; Linnea Hanson and Chris Christopherson (U.S. Forest Service) for securing permits and L. Hanson, Lawrence Janeway, and Lowell Ahart (CHSC) for field assistance during Rabeler's 2005 visit; and Carolyn Crawford for the illustration. We also thank the curators of CAS, CHSC, DAV, F, MO, PUA, UC/JEPS, and US for hospitality during visits and CAS, CHSC, F, NY, RSA, UC/JEPS, WTU, and Glenn Clifton for loans to RM or MICH and/or digital images of critical material.

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CASTILLEJA VICTORIAE (OROBANCHACEAE): A NEW RARE SPECIES FROM SOUTHEASTERN VANCOUVER ISLAND, BRITISH COLUMBIA, CANADA, AND THE ADJACENT SAN JUAN ISLANDS, WASHINGTON, U.S.A.

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ABSTRACT

Castilleja victoriae is described from the vicinity of southwestern Victoria, southern Vancouver Island, British Columbia, Canada and from San Juan Co., Washington, U.S.A. It is an annual member of subg. Colacus (Jeps.) T.I. Chuang & Heckard, sect. Oncorhynchus (Lehm.) T.I. Chuang & Heckard, formerly placed in the genus *Orthocarpus* Nutt. It is apparently most closely related to either *Castilleja ambigua* Hook. & Arn. or *Castilleja tenuis* (A. Heller) T.I. Chuang & Heckard. The new species differs primarily in its uniformly dull reddish-brown floral bracts and calyces, bicolored and unspotted corollas, and restrictive habitat requirements. Several historic populations are extirpated, and of the three extant populations only one consists of enough individuals in a protected location to be considered reasonably secure. We advocate additional surveys of its limited habitat and conservation measures to protect the species.

Key Words: British Columbia, *Castilleja victoriae*, Castillejinae, chromosome number, endangered species, new species, Orobanchaceae, Scrophulariaceae, Washington.

Specimens from a perplexing population of *Castilleja* were first collected in Victoria, British Columbia by J. Macoun in 1893 (*Macoun 722*) and were identified by him as *Orthocarpus castillejoides* Benth., a species now placed in the genus *Castilleja* Mutis ex L.f. (Chuang and Heckard 1991). Since that time, similar material was collected from nine other sites, all within 40 km of the first collection. Over the years, herbarium sheets from these collections have been variously identified in decreasing order of frequency as *O. castillejoides* (=*C. ambigua* Hook. & Arn. subsp. *ambigua*), *O. hispidus* Benth. (=*C. tenuis* (A. Heller) T.I. Chuang & Heckard), *O. pusillus* Benth. (=*Triphysaria pusilla* (Benth.) T.I. Chuang and Heckard), and *O. luteus* Nutt.

Divergent *Castilleja* populations in the vicinity of the city of Victoria were first noted in print by J. K. Henry (1915), who identified them as *Orthocarpus hispidus*, distinct from related plants found in the salt marshes of western Vancouver Island, which he identified as *O. castillejoides*. D. D. Keck (1927), in his comprehensive monograph on the genus *Orthocarpus* Nutt., followed Henry's interpretation, citing for Vancouver Island only a single collection of *O. castillejoides* (*Henry s.n.*), which is referable to *Castilleja ambigua*, and a single collection of *O. hispidus* (*Macoun 722*), which is a collection of the new taxon described below. In unpublished herbarium annotations following the publication of his monograph, Keck annotated different collections of the Victoria plants as *O. castillejoides* (*Eastham s.n.*, DAO), *O. hispidus* (*Macoun 722*, GH), or "*O. hispidus* [unusual form]" (*Newcombe s.n.*, WS). Keck's uncharacteristic difficulty in determining these plants is further indicated by an unsigned and undated annotation on a sheet housed at CAN (*Eastham 9843*), "This (is) apparently not typical, and Dr. Keck was at first inclined to consider it as possibly a new species. However with more material he finally referred it to *O. castillejoides*". A similar annotation is found on a sheet at DAO (*Eastham s.n.*). In Keck's defense, there is no indication that he ever saw the species described here in the field, where its unique characters are best appreciated. British Columbia floras (Taylor 1974; Douglas et al. 1991) have accepted the original, published interpretations of Henry and Keck.

Despite difficulties in assigning these collections to a known taxon, botanists familiar with the unusual populations around Victoria did not further question their identity, perhaps due in part to Keck's unpublished annotations. In 2004, while examining populations of *Castilleja ambigua* on the west coast of Vancouver Island, Fairbarns concluded that plants in the vicinity of

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Victoria were indeed unique and belonged to an undescribed taxon. Fortuitously, in June 2005, botanists collecting in support of a collaborative survey by the WTU Herbarium and The Nature Conservancy of the flora of the smaller islands throughout the San Juan Archipelago located the first United States population of the new species on a small islet adjacent to Lopez Island. Egger examined the new material shortly after viewing collections and photographs of the Victoria plants supplied by Fairbarns and immediately recognized their close similarity. A review by both authors of material collected from all known sites and field examination of thousands of plants in the three extant populations over two growing seasons revealed that the plants in question are distinct at the species level.

Castilleja victoriae *Fairbarns and J. M. Egger*, sp. nov. (Fig. 1)—TYPE: CANADA. British Columbia: vernal pool on W side of Trial Island, ca. 0.5 km from SE corner of city of Victoria, Vancouver Island, in low vegetation dominated by vernal pool annuals, slightly depressed site over shallowly buried bedrock, elev. ca. 4 m, 21 Jul 2005, *Matt Fairbarns s.n.* (holotype: WTU 363026; isotypes: CAN, US).

Latin diagnosis. Castillejae ambiguae Hook. & Arn. similis sed bracteis et lobis calycum non valde dissimilibus a foliis, interdum viridulis proximaliter ad obscure porphyreis distaliter, interdum obscure porphyreis undique, apicibus nunquam coloratis aliter; labiis abaxialibus corollarum lenibus citrinis, non maculatis, stigmatibus persaepe inclusis intra rostra corollarum. *Castillejae tenui* (A. Heller) T. I. Chuang & Heckard similis sed caulibus brevidecumbentibus ad ascendentibus, 5–15 cm altis, foliis ovatis ad lanceolatis, marginibus integris vel lobatis, lobis lateralibus 1vel 2 paribus, lanceolatis, plerumque obscure rubropurpureis ad porphyreis; bracteis interdum viridulis proximaliter et obscure porphyreis distaliter, interdum obscure porphyreis undique, lobatis, lobis 3–7, lanceolatis, apicibus plerumque triangularibus, tubis et rostris corollarum plerumque lenibus albis, labiis abaxialibus corollarum lenibus citrinis, non maculatis.

Plants annual with thin, weakly developed, straw-colored taproots, usually with several lateral rootlets. **Stems** usually solitary but occasionally with 2–4 branches from the base, these occasionally branched again below mid-point, upright to weakly ascending, dull reddish-brown, 2–20 cm long in flower, bearing a mix of short, gland-tipped hairs and longer, multicellular, pilosulous hairs. **Leaves** cauline, alternate, 0.5–2.7 cm long, generally dull reddish-purple to reddish brown throughout, sometimes pale greenish proximally grading into dull reddish-purple to reddish brown distally, pubescent throughout with a mix of short, gland-tipped hairs and longer, pilosulous hairs; lower leaves entire, lanceolate to narrowly ovate, often withering at anthesis; middle leaves 1.0–2.7 cm long, entire or more commonly with 1–2 pairs of ascending, short, lanceolate, acute-tipped lobes; upper leaves grading into the floral bracts, divided into 3–7 lanceolate lobes, these 8–12 mm long and 1–2 mm wide, generally wider and often longer than in the middle leaves, and with midlobes 1–4 mm wide. **Inflorescences** densely flowered, compact, bracteate spikes, 1–15 cm long. **Bracts** similar to upper leaves in most characters but ovate-lanceolate, usually imbricate, deeply 3–7-lobed, pale greenish proximally, quickly grading into dull reddish brown distally. **Calyces** 8–12 mm long, pale greenish throughout or pale greenish proximally, grading into dull reddish-brown distally, bearing a mix of gland-tipped and eglandular hairs, and deeply cleft into four linear-lanceolate lobes, the two primary lobes 5–6 mm long, each divided into two linear-lanceolate, acute segments, 3–4 mm long. **Corollas** bilabiate and clavate, 10–18 mm long, bicolored (yellow and white but appearing yellowish at a distance due to the prominently colored lower lips); lower lips trisaccate and somewhat expanded, about 3–5 mm long and 1–3 mm deep, with the middle lobe often infolded again creating two secondary lobes, 0.5–1.0 mm deep, soft lemon-yellow and unspotted, pubescent with a mixture of short, gland-tipped and eglandular hairs and slightly longer, eglandular, pilosulose hairs, and terminating in 3 inconspicuous whitish teeth, 0.5–0.8 mm long; beaks bilobed, lobes united to tip and enclosing the anthers, straight, surpassing the lower lip by 0.4–0.8 mm, white, very rarely with faint, diffuse purple shading, puberulent with a mix of short gland-tipped and longer eglandular hairs outside and eglandular hairs within; **stamens** four, didynamous, filaments 4.5–6.0 mm long, attached near summit of corolla tube, one pollen sac apically attached, the other versatile; stigmas entire, capitate, almost always included, minutely penicillate. **Mature capsules** slightly obcompressed, ovate-cuspidate, 5–6 mm long and 3–4 mm wide, loculicidal. **Seeds** averaging 60 per capsule (range: 37–80), short-ovoid, 0.9–1.3 mm long, stramineous and somewhat glassy, with terminal hilum; coats loose-fitting, reticulate, cells mostly polygonal-ovate, radial walls shallow, smooth or with obscure horizontal striations, inner tangential walls membranous, smooth, more or less opaque, unruptured at maturity. **Chromosome number** $2n = 24$, photographic images of pollen mother cells in diakinesis on file at WAT and WTU.

Common names. Victoria's Owl's-clover, Victoria's Paintbrush.

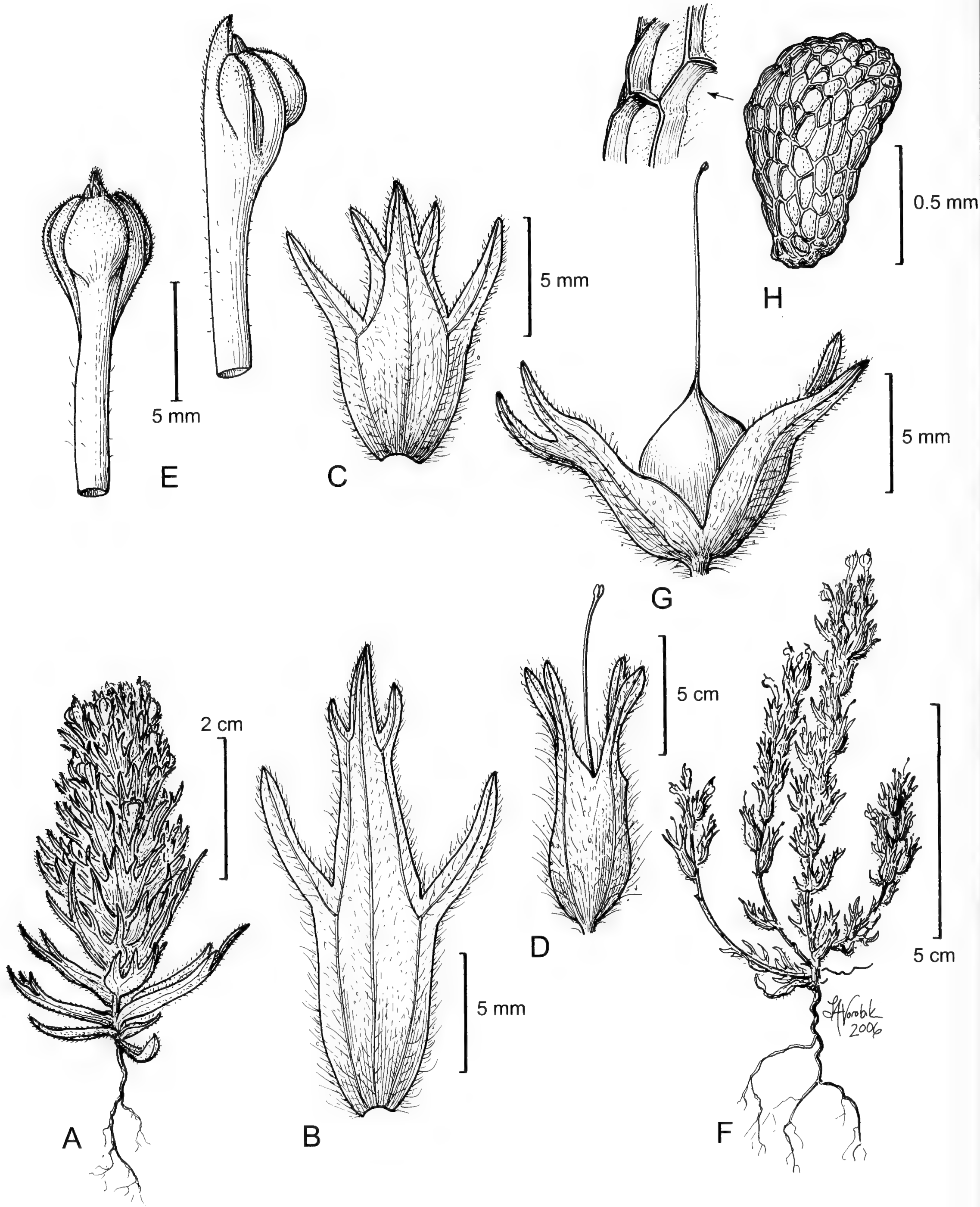

FIG. 1. *Castilleja victoriae* Fairbarns & J.M. Egger. A. Habit in flower: typical, single-stemmed plant. B. Leaf. C. Floral bract. D. Calyx, stigma and style. E. Corolla, ventral view (left), lateral view (right). F. Habit in late flower and fruit: infrequent, multi-stemmed plant. G. Partially dissected calyx and mature capsule. H. Seed with detail of seed coat. Based on *Fairbarns s.n.* (WTU).

Etymology and dedication. This species is named in memory of Victoria Zessin of Nebraska and Oregon, whose too brief life was a beautiful inspiration to those who knew her, and also for the city near which it was first discovered.

Additional specimens examined. CANADA. British Columbia: Vancouver Island: Victoria: Dallas Hotel, Beacon Hill, 7 Aug 1893, *Macoun 722* (CAN, GH); "Fowl Bay" [=Foul Bay], 18 Aug 1893, *Macoun 721* (CAN); Oak Bay, 8 Jul

1898, *Anderson 715* (V, WS), 5 Jun 1908, *Macoun 87708* (CAN, NY), 9 Jun 1919, *Newcombe s.n.* (V, 2 sheets; WS); Cattle Point, along Marine Drive, Uplands Park, 25 May 1961, *Calder & MacKay 29531* (DAO, UC, WTU), 21 Jun 1961, *Calder & MacKay 30757* (DAO, UC), 20 Jul 1966, *Harrison 90.1* (CAN, V), 5 Jun 1976 *Ceska & Ceska 27824* (V), 24 Jun 1976, *Armstrong & Armstrong s.n.* (V), 7 Jul 1993, *Ryan 63* (V); grown in pots from seed collected at Cattle Pt., 25 Jul 1975, *Armstrong & Armstrong 9* (V); Uplands Park, dry vernal pool areas near coast, 10 Jun 1960, *Melburn s.n.* (V), 22 May 1961, *Melburn s.n.* (DAO); Ten Mile Point, 21 May 1939, *Hardy s.n.* (CAS-DS, UBC, V), 12 May 1940, *Hardy & Hardy s.n.* (CAS-DS), 21 May 1940, *Eastham 7156* (DAO, UBC), 21 May 1940, *Hardy & Eastham s.n.* (CAS-DS, UVIC, V, WTU), 28 Apr 1941, *Hardy s.n.* (UVIC), 11 May 1941, *Hardy s.n.* (CAS-DS, V), 22 May 1942, *Eastham 9843* (CAN, UBC), 13 Jun 1945, *Eastham s.n.* (DAO), 13 Jun 1945, *Hardy s.n.* (V), 24 May 1954, *Melburn s.n.* (V). Shawnigan area: 8 Jun 1957, *Melburn 6162* (UVIC, 2 sheets). Greater Trial Island: 20 Jul 1976, *Ceska & Ceska s.n.* (V), 9 Jul 1981, *Ceska 6459* (V). Lesser Trial Island: 11 Jun 1953, *Hardy s.n.* (V). Chain Islands: 24 Jun 1923, *Newcombe s.n.* (V). UNITED STATES. Washington: San Juan Co.: San Juan Islands National Wildlife Refuge, in single dry vernal pool, (near Lopez Island, precise location data removed for conservation reasons), 29 May 2005, *Bellefond 05-36* (WTU).

Distribution. This new species is known primarily from the vicinity of Victoria, British Columbia (Fig. 2). The sole United States population occurs on a small island adjacent to Lopez Island, San Juan County, Washington, while all other populations occur on or adjacent to southern Vancouver Island, British Columbia. The site in the San Juan Islands is about 30 km east, directly across the Haro Strait from the Vancouver Island populations. The northernmost reported location, in the Shawnigan area, (*Melburn 6162*) is doubtful and may be based on an erroneous herbarium label, as field studies at the location described failed to discover any plants or suitable habitat.

Reproduction and phenology. Castilleja victoriae is an out-crosser, pollinated by bumblebees (*Bombus* sp.) and perhaps other insects. Seeds appear to require a period of cold weather before they germinate. Close study of two Canadian populations revealed that neither fresh nor banked seeds germinate after late summer rains, even if temperatures remain warm (Fairbarns, unpubl. data). *C. victoriae* begins to germinate in early April, although most seedlings do not appear until late April or early May. The seedlings grow slowly in the cool, wet soil. Mortality appears to be high among young seedlings, but most plants reaching the six-leaf stage survive until the summer dry season kills the entire cohort. Maturing plants bloom in May and June, and seed ripens in late June through July. Capsules begin to dehisce in June, and seeds are gradually dispersed through the summer and autumn, as they are shaken from the partially opened capsules. Seed dispersal ends abruptly when autumn storms break down the dead shoots. Most dispersed seeds remain close to the parent plant.

Habitat and associated species. Castilleja victoriae is restricted to coastal freshwater seeps and very shallow ephemeral pools on thin soil over gneissic bedrock knolls and benches. It only occurs close to the ocean, where winter frosts are light and infrequent. It is restricted to open areas where wind, salt spray, shallow soils and waterlogged conditions in winter restrict the growth of woody plants and large perennial herbaceous species. All populations occur within 1–5 m above sea level and within 50 m inland from the sea. No single species occurs consistently in the vicinity of *C. victoriae*, which suggests it is not species-specific in its presumed root hemiparasitism. This is true of most other species of *Castilleja* for which such data have been collected (Heckard 1962). Commonly associated species include *Aira caryophyllea* L., *Armeria maritima* (Miller) Willd., *Grindelia* sp., *Festuca rubra* L., *Hypochaeris radicata* L., *Lotus unifoliolatus* (Hook.) Benth., *Montia fontana* L., *Plagiobothrys scouleri* (H.&A.) I.M. Johnst., *Plantago elongata* Pursh, *Plantago maritima* L., *Prunella vulgaris* L., *Silene gallica* L., and *Trifolium depauperatum* Desv.

Relationships and Identification

The genus *Castilleja* was formerly placed in the family Scrophulariaceae, but recent molecular studies summarized in Olmstead et al. (2001) have confirmed its placement in a monophyletic Orobanchaceae. Within the Orobanchaceae, *Castilleja* belongs to subtribe Castillejinae G. Don. Based on morphology and duration, *Castilleja victoriae* is easily placed with the annual species of *Castilleja* subg. Colacus (Jeps.) T. I. Chuang & Heckard, sect. Oncorhynchus (Lehm.) T. I. Chuang & Heckard (Chuang and Heckard 1991). Species of this assemblage are found primarily in western North America, with a secondary radiation in the central Andes Mountains of South America (Chuang and Heckard 1991, 1992; Tank 2006) and are characterized by annual duration, pollination by insects, primarily bees, reduced corolla beak, and more or less inflated lower corolla lip. *Castilleja victoriae* occurs near the northern range limit of this

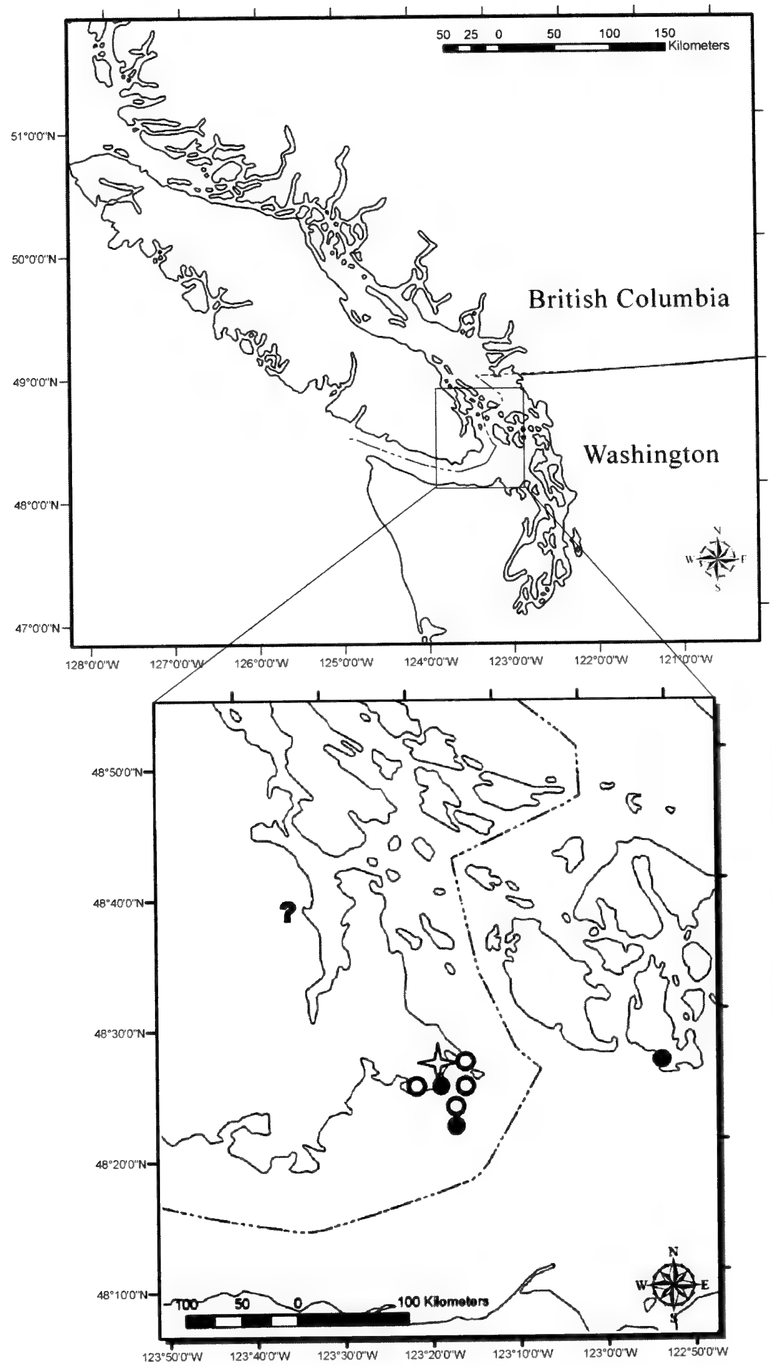

FIG. 2. Range of *Castilleja victoriae* with detail showing distribution on and adjacent to southwestern Vancouver Island, Canada. Open circles indicate historic, extirpated populations. Solid circles indicate extant populations. Star indicates a recently extirpated population. Question mark indicates a doubtful collection location (see text).

species group. Preliminary phylogenetic analyses of chloroplast and nuclear ribosomal DNA sequence data indicate that *C. victoriae* is most closely related to *C. ambigua* and may be recently derived from that morphologically similar species (D. C. Tank, unpubl. data).

In partial concordance with the preliminary molecular data, *Castilleja victoriae* is morphologically most similar to *C. ambigua* and *C. tenuis*. It has been confused frequently with both species and shares several characters with each but in a unique combination. The similarities between

these three species are probably not due to allopolyploid hybridization, as the new species has a chromosome number of n = 12, the base number for this genus (Chuang and Heckard 1991). Of its relatives occurring in the Pacific Northwest, *C. ambigua*, *C. attenuata*, and *C. tenuis* are all known from counts of n = 12, while some populations of *C. tenuis* are also known to be polyploid, with counts of n = 24 (Chuang and Heckard 1982). Additional DNA and chromosome sampling of extant populations of *C. victoriae* and related species would be informative.

In the field, *Castilleja victoriae* is easily distinguished from related species, even at a distance, by its unique combination of short, compact aspect, usually single-stemmed growth form, largely uniform, "root-beer" brown herbage, floral bracts more lobed but otherwise like the leaves, without contrasting coloration on the bract tips, and distinctively bicolored, unspotted corollas (Fig. 3). These characters, along with a specialized habitat and limited distribution, assure its recognition in living populations. While the plants are far less distinctive when pressed and dried, careful examination of the inflorescence will easily separate *C. victoriae* from all but a few atypical and faded specimens of *C. ambigua* and more easily still from other related species.

Two characters are useful in distinguishing *Castilleja victoriae* from *C. ambigua* but did not fit conveniently into either the key below or the diagnosis. First, most plants of *C. victoriae* consist of a single, unbranched stem. Among specimens counted on all sheets of *C. victoriae* examined (n = 342 individuals), 90.4% were unbranched, and 97.4% had three or fewer stems, all of which were unbranched above the base. Of the 2.6% that contained more than three branches at the base, several were branched again between the base and mid-stem. One exceptional individual (*Eastham 722*, CAN) contained a total of 16 inflorescences branching from four basal stems. Photographic field data from all three extant populations confirm the predominance of single-stemmed plants in *C. victoriae* (Egger, unpubl. data). Except in one or two cases, the branching of the stems did not appear to be the result of cropping through herbivory. While the occurrence of single-stemmed plants is not unknown in *C. ambigua*, most plants of that species have numerous decumbent to ascending stems (Egger, unpubl. data). Secondly, the seed coats of *C. victoriae* are straw-colored, somewhat glassy, more or less opaque, and loose fitting. Those of *C. ambigua* are darker, more or less transparent, and tight fitting.

The following key can be used to distinguish *Castilleja victoriae* from closely related species occurring in the Pacific Northwest, north of the Siskiyou region of southern Oregon.

Key to the Annual Species of *Castilleja* Subg. Colacus, Sect. Oncorhynchus Native to Northern Oregon, Washington, and British Columbia.

1. Coloration of floral bracts strongly differentiated from leaves, almost always greenish with lobe tips strongly contrasting in color, white or less commonly yellow or pink-violet; tips of calyx lobes often strongly contrasting in color, as in floral bracts; lower lip of corollas usually marked with small reddish-purple spots near base of apical teeth; stigmas exserted from tip of corolla beak (*C. ambigua*) or included within beak (*C. attenuata*) 2

1. Coloration of floral bracts not strongly differentiated from leaves, more or less uniformly colored either entirely green, green proximally grading into dull reddish brown distally, or entirely dull reddish brown, with lobe tips not strongly contrasting in color; tips of calyx lobes never strongly contrasting in color; lower lip of corolla either entirely unspotted or with obscure, dull-reddish spots near base; stigma almost always included within corolla beak 3

   2. Plants usually much branched with stems decumbent; leaves lanceolate to ovate; bracts oblong to ovate, divided into 3–9 lanceolate lobes; lobes of lower corolla lip inflated to form pouches 3–7 mm wide; stigmas usually exserted from tip of corolla beak; in our region plants strictly limited to outer margins of tidal salt marshes or sandy hollows along coast and rarely in Puget Sound . . . . *Castilleja ambigua*

   2. Plants unbranched or few-branched from near base with stems upright to ascending; leaves more or less linear; bracts lanceolate, divided into 3 linear-lanceolate lobes; lobes of lower corolla lip slightly inflated to form pouches 1–2 mm wide; stigmas usually included within corolla beak; plants of lower elevation grasslands, meadows and openings, never in tidal salt marshes or sand dunes . . . *Castilleja attenuata*

3. Leaves linear-lanceolate with 0–5 linear lobes; bracts usually pale greenish throughout or sometimes pale green proximally grading into dull reddish-purple in the distal half, with 3–7 linear-lanceolate, narrowly acute-tipped lobes; corollas uniformly colored either white or yellow, usually with obscure, dull-reddish spots near base of lower lip; never coastal, occurring east of crest of Cascade Mountains in Washington and British Columbia . . . . *Castilleja tenuis*

3. Leaves ovate to lanceolate with 0–5 lanceolate lobes; bracts usually dull reddish-brown throughout or pale greenish proximally, becoming dull reddish brown distally, with 3–7 lanceolate, broadly acute-tipped lobes; corollas appearing yellow at distance but bicolored, with tube and beak pale white and lower lip soft lemon-yellow, unspotted, with pale white apical teeth; plants endemic to vernally moist depressions in shallow soils over rock above

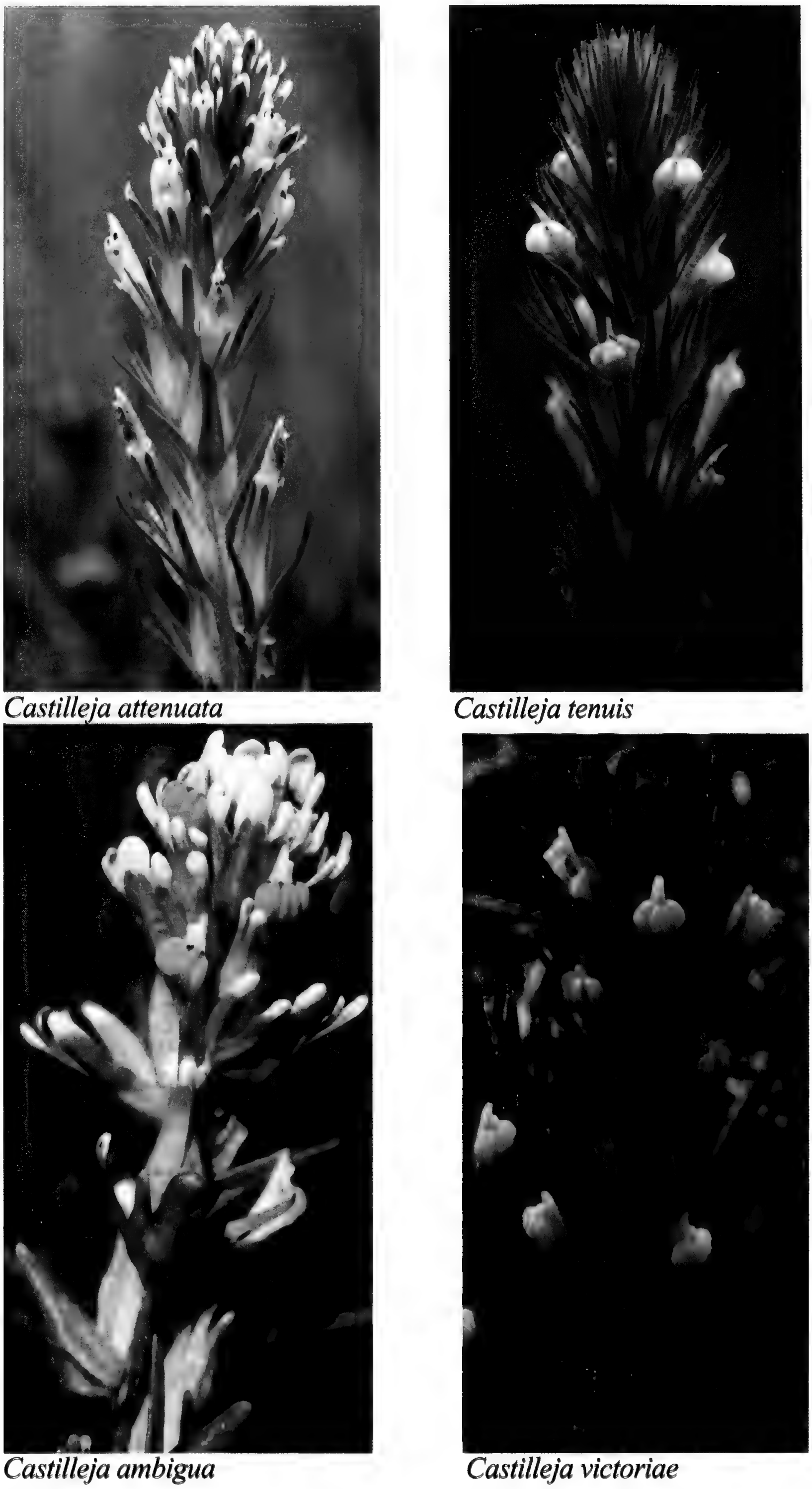

FIG. 3. *Castilleja victoriae* and related species. Photographs by Mark Egger.

shoreline on islands bordering Haro Strait region of Puget Trough. . . . . . *Castilleja victoriae*

Conservation Status

Castilleja victoriae is known from only three extant populations. A fourth population, occurring in a similar situation, dwindled in numbers over the past decade and has not been seen during the past five years (through 2007), despite frequent careful surveys throughout its growing season. Four other known populations have been extirpated since the late 1800s by suburban expansion from the growing city of Victoria and resulting destruction and deterioration of habitat. As well as direct development, tourist and recreation-related activities and invasive weeds also appear to have played a significant role in the decline of this species. Extensive surveys of suitable and marginally suitable habitat at over 80 sites on and adjacent to southwestern Vancouver Island from 2003–2006 (Fairbarns, unpubl. data), as well as similar surveys in the San Juan Islands in Washington from 2005–2006 (The Nature Conservancy, unpubl. data), failed to locate any additional populations beyond those documented here.

Much of the remaining habitat suitable for *Castilleja victoriae* has been heavily altered due to invasion and overtopping by alien weeds, including several grasses (*Agrostis capillaris* L., *Aira praecox* L., *Anthoxanthum odoratum* L., *Bromus hordeaceus* L., *Dactylis glomerata* L., *Holcus lanatus* L., *Hordeum* spp., *Lolium perenne* L., *Poa annua* L., *Vulpia bromoides* (L.) S. F. Gray) and forbs (*Bellis perennis* L., *Geranium molle* L., *Hypochaeris glabra* L., *H. radicata* L., *Plantago lanceolata* L., *Rumex acetosella* L., *Silene gallica* L., *Spergularia rubra* (L.) J. & K. Presl).

In 2006, the three extant populations of *Castilleja victoriae* occupied a collective area of 600–700 m^2 and numbered approximately 7000–8000 individuals. Of these, many failed to produce viable seed. The great majority of these plants occur at a single site, while the other two populations numbered 164 and 31 plants, respectively. The populations are limited by suitable micro-site habitat within the species' range, as well as by apparently poor dispersal ability and recruitment. The latter factor may be at least partially due to a lack of suitable host plants in some areas, but this remains conjectural without better knowledge of which species are utilized as hosts by *C. victoriae*. The smallest population occurs in a heavily used natural area within a residential neighborhood of Victoria and is subject to trampling and disturbance by humans and domestic animals. Historically, grazing of domestic sheep in the archipelago may have also been a factor in the present rarity of *C. victoriae*.

In 2006, the authors noted instances of vertebrate herbivory in the San Juan Islands population affecting a number of individuals of *Castilleja victoriae*. Due to the manner of cropping and the isolated nature of this small island habitat, the herbivory was likely due to grazing by Canada Geese, *Branta canadensis* (L.), populations of which are rapidly increasing in this region (Kraege 2005). Herbivory by Canada Geese has also been noted by Fairbarns in the Canadian populations of *C. victoriae*. In these cases, either corollas were picked off or entire inflorescences were cropped, substantially reducing or effectively eliminating the plants' ability to set seed. Canada Geese are thought to be the cause of severe degradation in the flora of other nearby islands (P. Dunwiddie, The Nature Conservancy, personal communication, 2006). No debilitating herbivory by invertebrates was observed in any of the populations. Insects occasionally bore through floral bracts, but none of 380 capsules examined in 2002 and 2003 were perforated. No fungal damage was observed in any plants in detailed studies of two Canadian populations over three years (Fairbarns, unpubl. data).

Due to the small numbers of remaining populations and individuals, very narrow geographic and edaphic distributions, vulnerability to herbivory, habitat degradation by human activities, invasive weeds, and potential stochastic events, such as sea level changes, this species' long-term survival is at risk. *Castilleja victoriae* should be evaluated immediately for listing and protection under endangered species laws in both countries, and additional field surveys are needed, especially in the San Juan Islands of Washington.

Plants of *Castilleja victoriae* have been brought to seed successfully in the Victoria region under cultivation in pots. A sample of these cultivars is documented with a herbarium sheet (*Armstrong & Armstrong 9*, V), though the precise growing techniques employed have not been recorded. This suggests that cultivation may potentially provide an additional source of seeds for introduction in areas with suitable habitat and for other conservation purposes.

Acknowledgments

We extend our sincere appreciation to Linda A. Vorobik for her skillful preparation of the drawing, to John L. Strother and Alan R. Smith (UC/JEPS) for editing the diagnosis and translating it into Latin, to John C. Semple (WAT) for the chromosome counts, and to Katrina Stipec (British Columbia Conservation Data Centre) for assistance in preparation of the range maps. We also thank John Pinder-Moss (V) and David E. Giblin (WTU) for assistance with loans and other herbarium-related matters and Adolf Ceska (V) for informative discussions. We thank David Giblin, David C. Tank (Y), and Peter C. Zika (WTU) for their useful

critiques of earlier drafts of the manuscript and two anonymous reviewers for their valuable comments. Appreciation is also extended to the personnel of the following herbaria for assistance with loans for this study: CAN, CAS, DS, CM, DAO, GH, MO, NY, ORE, OSC, UBC, UC, US, UVIC, V, WILLU, and WS, WTU. For assistance accessing remote locations, we thank Peter Dunwiddie (The Nature Conservancy), Robert Fimbel (Washington State Parks), David Giblin, Sarah Joanisse (British Columbia Parks), Richard Olmstead (WTU), and Deaydra Wise (Washington State Parks). Finally, special thanks are extended to Margriet Wetherwax for bringing the authors into contact, facilitating the recognition of this unique new species.

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PENTACHAETA AUREA SUBSP. *ALLENII* (ASTERACEAE), A NEW SUBSPECIES FROM ORANGE COUNTY, CALIFORNIA

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ABSTRACT

Pentachaeta aurea Nutt. subsp. **allenii** Keil is described as new. It is apparently endemic to southwestern Orange Co., California. Lamina tips of ray corollas of living specimens of the plants are pale yellow in early morning but turn brilliant white after 1–2 hr in sunshine; laminae of subsp. *aurea* are solid yellow.

Key Words: Asteraceae, Limestone Canyon Wilderness Park, Orange County, *Pentachaeta aurea* subsp. *allenii.*

During fieldwork preparation for a book on the wildflowers of Orange County and the Santa Ana Mountains, Mr. Robert Allen encountered an unfamiliar member of the Asteraceae. After examining his photograph and specimens that he had collected, I determined that the plants represent a distinctive subspecies of *Pentachaeta aurea*.

Pentachaeta aurea Nuttall subsp. **allenii** Keil, subsp. nov.— Type: U.S.A. CA, Orange Co., Lomas de Santiago, Limestone Canyon Wilderness Park, Limestone Canyon, on gentle south-facing hillside with *Castilleja exserta*, *Linanthus dianthiflorus*, *Erodium* spp., and introduced *Bromus* grasses; the area burned extensively in 1998; 12 Apr 2003, *Robert L. Allen s.n.* (holotype OBI; isotypes CSUF, RSA, UC).

Laminis flosculorum radiorum bicoloratis duabus tertiis partibus distalibus albis et modo tertia parte proximale aurea a subsp. *aurea* distinguitur.

Annual, 20–35 mm. *Stems* slender, erect, pale reddish brown, glabrous; *branches* ascending, overtopping main stem. *Leaves* alternate, linear, entire, 2–5 cm, 1–1.4 mm wide, distally diminishing to linear bracts, surfaces glabrous, margins inconspicuously villous-ciliolate with fine, septate hairs. *Capitulescence* corymbiform; peduncles elongated, slender, terminating main stem and branches, distally slightly expanded and thinly villous, otherwise glabrous. *Capitula* radiate; receptacles epaleate, slightly convex, glabrous; *involucres* narrowly campanulate, glabrous; *phyllaries* graduated in 3–4 series, the outer oblong, 3–5 mm, the inner linear ± 8 mm, each with scarious margins about equal in width to the green, medial zone, the green center exceeding the scarious margins by 0.5–1 mm, tapering to an awn-like tip. *Ray florets* 30–45, fertile; *corollas* 11–14 mm; *tubes* 2.5–3 mm, whitish or reddish tinged, with reddish veins; *laminae* narrowly elliptic, distally narrowed, minutely 3-lobed, bicolored, the proximal third yellow, the distal two thirds white (drying cream), reddening in age; *style branches* 1.5 mm, linear, slightly exserted from corolla tube. *Disk florets* many, fertile; *corollas* tubular, 4.5–6.5 mm, of variable length within a capitulum; *tube* 0.5–1 mm, scarcely differentiated externally from throat; *throat* 2.5–4 mm; lobes ± lanceolate, 1.5 mm; tube and lower throat pinkish to light purple, upper throat and lobes yellow; *anthers* ± 1.5 mm, retained deep within corolla throat, not tailed, with short, awn-like terminal appendages; *style branches* linear, 2–2.5 mm, appendages narrowly cylindric, 1–1.7 mm, hispidulous; stigmatic portion ± 1 mm, wider than appendages, smooth. *Ray and disk cypselae* similar, clavate, slightly stipitate at base, 1.5 mm, ±1.5 mm diameter, terete, with 4–6 narrow lobes, dark brown, puberulent with short, ascending white trichomes; *pappus* of 4–6 stiff bristles, these slightly enlarged at base, 3–4 mm, widely spreading at maturity, minutely barbed, brownish.

DISTRIBUTION, HABITAT, AND PHENOLOGY

Pentachaeta aurea occurs in southwestern California and northwestern Baja California (Lane 1993; Van Horn 1973). It is known from the coast to the lower elevations of the Transverse and Peninsular ranges. In California it ranges from southeastern Los Angeles County and southwestern San Bernardino County south through Orange, western Riverside, and western San Diego Counties.

Subspecies *allenii* is known only from southwestern Orange County where its range is nested within that of subsp. *aurea*. It was photographically documented from a coastal site at Dana

Point in 1983 by Fred Roberts (Robert Allen, Research Associate, Rancho Santa Ana Botanic Garden, personal communication), about 20 mi southeast of the type locality. Mr. Allen relocated and photographically documented a very small population at Dana Point in the spring 2003 and 2004, and Fred Roberts took vouchers. However, in early 2006, nearly the entire Dana Point headlands was bulldozed to make way for a housing development, including the spot where the plants had been growing.

The habitat at the type locality is a grassland dominated by introduced Mediterranean grasses with a mixture of native and introduced forbs. The plants were in full bloom in mid-April.

Biology

In features other than their bicolored ray laminae, plants of subsp. *allenii* fall well within the range of variability of *P. aurea*. The white tips of the ray laminae of subsp. *allenii* apparently change color in response to sunlight. Gene Jones and Robert Allen noted that the lamina tips of living specimens of the plant were pale yellow in early morning but turned brilliant white after 1–2 hr in sunshine (Robert Allen, personal communication). The original photo Mr. Allen sent me showed the brilliant white lamina tips, but in herbarium specimens these are cream-colored. Van Horn (1973) noted that rays of *P. aurea* range from pale yellow to burnt orange (rarely white). He indicated that his report of a white-rayed form of *P. aurea* was based upon a specimen collected in 1910 at a train depot near El Toro (*Payne s.n.*, UC). Van Horn noted that rays of the dry specimen appeared very pale yellow and probably were white when collected. El Toro is about halfway between the type locality and Dana Point. Robert Allen (personal communication indicated that the white distal region of the rays of the Dana Point plants is overall smaller than in the plants from Limestone Canyon. Nesom (2006) treated *Pentachaeta* for the *Flora of North America North of Mexico*. Nesom's description of *P. aurea* made no mention of white or bicolored ray laminae.

Rarity

Pentachaeta aurea subsp. *allenii* is known only from southern Orange County. The type locality is on land managed by The Nature Conservancy. Protection status of other populations is unknown. The El Toro population is probably no longer extant, and the Dana Point population has probably been extirpated. In view of the development history of Orange County, any plant known from only a few localities should be considered for listing by appropriate private and public agencies.

Acknowledgments

I thank my friend Robert Allen for bringing this plant to my attention and for his follow-up work on gathering data and enabling me to obtain material of subsp. *aurea* for comparison. Dr. Guy Nesom provided comments on an early version of this manuscript. Dr. Judy Gibson (San Diego Natural History Museum) supplied material of subsp. *aurea*.

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A NEW SUBSPECIES OF *PENTAGRAMMA TRIANGULARIS* (PTERIDACEAE)

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Abstract

Pentagramma triangularis (Kaulfuss) Yatskievych, Windham, & E. Wollenweber subsp. **rebmanii** Winner and M. G. Simpson subsp. nov. is a new subspecies endemic to south-central to southeast San Diego County, California, USA, and inland, northwestern Baja California, Mexico. It is uncommon on seasonally moist, granitic-derived or gabbro-clay substrates, distinguishable from other *Pentagramma triangularis* subspecies by the scattered white farina on the adaxial blade surface and lightly scattered along the stipe.

Resumen

Pentagramma triangularis (Kaulfuss) Yaskievych, Windham, & E. Wollenweber subsp. **rebmanii** Winner and M. G. Simpson subsp. nov. es una subespecie endémica del centro-sur al sureste del Condado de San Diego, California, Estados Unidos de America, y del interior noreste de Baja California, México. Esta planta poco común crece sobre tierras estacionalmente húmedas derivadas de granito o de gabro, y es distinguible de otras subespecies de *Pentagramma triangularis* por la presencia de farina blanca desparramada en la superficie adaxial de la lámina y ligeramente por todo el estípite.

Key Words: Baja California, Mexico, *Pentagramma*, Pteridaceae, San Diego County, California, USA.

San Diego County, California, has an exceptionally diverse flora for an area of its size, containing 2314 vascular plant taxa; 1735 taxa or 71% of the total are native (Rebman and Simpson 2006). Included among these are 29 taxa (27 species) of leptosporangiate ferns (=Polypodiopsida, *sensu* Smith et al. 2006); 28 of which are native. Thus, the leptosporangiate ferns of San Diego County constitute 1.2% of the total vascular flora and 1.6% of the native vascular flora. The adjacent Baja California peninsula of Mexico constitutes a much larger area and is considerably more diverse, with over 4000 total vascular plant taxa and nearly 30% endemism (Rebman 2006). Of these taxa, 70–75 leptosporangiate ferns (Mickel and Smith 2004) comprise approximately 1.7% of the total vascular flora. A comparable number of leptosporangiate fern taxa (ca. 75) and overall species endemism (30.6%) occurs in the state of California (Hickman 1993).

We describe here a new leptosporangiate fern subspecies, currently known only from south-central to southeastern San Diego County, California, and from inland, northwestern Baja California, Mexico. This new taxon adds to our knowledge of the biodiversity of these floristically rich regions.

Pentagramma triangularis (Kaulfuss) Yatskievych, Windham, & E. Wollenweber subsp. **rebmanii** Winner and M. G. Simpson subsp. nov.—**Type:** USA, SAN DIEGO COUNTY, CALIFORNIA: Cleveland National Forest, Pine Creek Wilderness, north of Barrett Lake and south of Descanso, east of Japatul Valley Road, southeast of Horsethief Canyon Trailhead and just west of Pine Valley Creek, north-facing slope, 32.7442°N, 116.6533°W, 610 m, 23 March 2005, *J. Rebman 11483 and G. Bustillos* (holotype: SD 159328; isotypes: BCMEX, RSA, UC).

Paratypes (see Fig. 4 for locality map): USA, SAN DIEGO COUNTY, CALIFORNIA: 8 mi E of Jamul, 0.6 mi E of Lawson Peak, 1 mi NNW of intersection Lyons Valley Road and Carveacre Road, 32.7258°N, 116.7158°W, 29 May 2005, *J. Barth 529* (SD 160835); Cuyamaca Rancho State Park, Descanso quad T15S, R4E, Sweetwater River near Merrigan Falls, 24 March 1986, *M. Curto 254* (SD 121002); Warrens Ranch, Campo, 22 April 1920, *A. Eastwood s.n.*

(CAS 92550, CAS 92554); below Morena Dam, 12 March 1936, *F. Gander 727* (SD 13923); 3 mi W of Canyon City, 7 April 1936, *F. Gander 1149* (SD 14364); Hipass, 12 May 1936, *F. Gander 1875* (SD 15294); La Posta, Old Highway 80, 0.1 mi W of intersection with Miller Valley Road, 32.7112°N, 116.3874°W, 13 February 2005, *J. Gregory 1251* (SD 160825); La Posta, Old Highway 80, 0.1 mi W of intersection with Miller Valley Road, 32.7112°N, 116.3874°W, 13 February 2005, *J. Gregory 1252* (SD 160824); Barrett Lake, near W shore on Barrett Lake Road, 3 mi SE of junction with Lyons Valley Road, 32.6823°N, 116.6758°W, 8 May 2007, *J. Gregory 2321* (SD 175902); Cleveland National Forest, W of Cuyamaca Mountains, ca. 4 mi S of intersection Eagle Peak Road and road to Deadman Flat, 33.0468°N, 116.6813°W, 1 April 2007, *J. Hirshberg 1361* (SD 175764); along trail below Morena Dam, 12 April 1963, *Larry Kiefer 511* (CAS 931205); Bratton Valley, 3 mi N of Delzura, 2.5 mi SE of Lyons Valley Peak summit, 0.5 mi S of intersection Honey Springs Road and Deerhorn Valley Road, 32.675°N, 116.7478°W, *J. Maxted 395* (SD 175857); Tecate Mountain, S side, 32°34.5′N, 116°41′W, 26 April 1969, *R. Moran 15845* (SD 74734); Cleveland National Forest (Descanso District), 1 mi SE of Lawson Peak, along Carveacre Road, 0.7 mi NW of intersection with Japatul Valley Road, 32.7163°N, 116.711°W, 19 May 2005, *M. Mulligan 1086* (SD 164908); Cottonwood Creek, 10 May 1924, *P. Munz 8029* (POM 48058); N base of Tecate Mountain, 15 March 1931, *P. Munz 11961* (POM 183678, UC 494522); Hauser Canyon Wilderness Area (USFS), N of Hauser Mountain, SW of Morena Lake, NW of Cameron Corners, 32.6714°N, 116.5697°W, 9 May 2003, *J. Rebman 8919* (SD 157262); Viejas Mountain, N of Alpine, 32.8703°N, 116.7331°W, 17 June 2004, *J. Rebman 10584* (SD 157261); Walker Canyon Ecological Reserve between Boulevard and Jacumba, N side Interstate 8, near E side of reserve, 32.6622°N, 116.2103°W, 2 December 2004, *J. Rebman 10766* (SD 157264); Viejas Mountain, N of Alpine, USFS land E of Kelley/Rebman Ranch, 32.8789°N, 116.7317°W, 27 February 2005, *J. Rebman 10980* (SD 158368); Walker Canyon Ecological Reserve (CAF&G) between Boulevard and Jacumba, N side Interstate 8, E side of Reserve, 32.6614°N, 116.2089°W, 22 March 2005, *J. Rebman 11389* (SD 158877, SD 159329, UCR); Cleveland National Forest, Poser Mountain, NE of Alpine and Viejas Indian Reservation, N of Old Viejas Grade Road, 32.8694°N, 116.6739°W, 19 April 2007, *J. Rebman 13114* (SD 175765); Potrero Peak, N of Tecate, 32.6241°N, 116.6271°W, 4 May 2007, *J. Rebman 13330* (SD 175766); Barrett Lake, S of dam, E of Barrett Lake Road, 32.6786°N, 116.6714°W, 8 May 2007, *J. Rebman 13488* (SD 175767); Campo, May 1916, *F. Stephens s.n.* (SD 9353); near Campo, 30 December 1922, *I. Wiggins 1045* (DS 506985, POM 180494); Kitchen Creek 4 mi N of Cameron, 32°45′N, 116°27′W, 3 October 1971, *H. Witham 1608* (SD 83813); 11 mi SW of Campo, Hwy. 94, T18S R3E S13, 27 May 1982, *G. Yatskievych 82-166*, (ASU 126433). MEXICO, STATE OF BAJA CALIFORNIA (=Baja California Norte): About 5 mi SW of river at Rancho Mike between Highway 3 and Parque Nacional Sierra de San Pedro Martir, 22 May 1981, *T. F. Daniel 1529* (ASU 116042); Sierra Blanca (based on R. Moran's subsequent correction in field notes; original label states Cerro Blanco as locality), NW slope, 32°3.5′N, 116°31′W, 24 May 1970, *R. Moran 17577* (SD 75789); Kumeyaay Ranch of Ha-a, 25 km ± SE of Tecate, 32°22′N, 116°30′W, 10 October 1976, *R. Moran 23777* (SD 97390).

Latin Diagnosis: Pentagramma triangularis (Kaulfuss) Yatskievych, Windham, & E. Wollenweber subsp. *semipallida* (J. T. Howell) Yatskievych, Windham, & E. Wollenweber simile, sed farina sparsa alba in adaxiali pagina laminae.

English Diagnosis: Similar to *Pentagramma triangularis* (Kaulfuss) Yatskievych, Windham, & E. Wollenweber subsp. *semipallida* (J. T. Howell) Yatskievych, Windham, & E. Wollenweber, but with scattered, white farina on the adaxial blade surface.

Rhizome decumbent, occasionally erect; densely covered with glossy, narrowly triangular to linear, fibrillose (*sensu* Lellinger 2002) (Fig. 3B), bicolorous scales, amber with a dark red-brown central, vertical stripe (Figs. 3A, B). **Fronds** (Fig. 1A), few to many (4–37+) per plant, 5–36 cm long, 3–14 cm wide. **Stipe** 3–28 cm long, slender (Fig. 1C), 0.25–1.75 mm wide, glossy red-brown (Fig. 3E), aging dull, dark red-brown; terete with a single, V-shaped vascular bundle (Fig. 3D), sparse white farina throughout, more dense proximally and distally, not viscid-glandular, with proximal rhizome-like or clathrate, lance-ovate scales (*sensu* Lellinger 2002), some scales at mid-stipe more deltoid-ovate either bicolorous amber with a dark red-brown mid-stripe, a dark red-brown apex (Fig. 3C), or concolorous amber. **Blade** (delineates everything above the stipe) herbaceous to somewhat coriaceous, deltoid-pentagonal (Fig. 1C), bipinnate-pinnatifid, the two basal pinnae subsessile (Figs. 1A, C), the proximal basiscopic lobes of basal pinnae deeply pinnate-pinnatifid (pedate, *sensu* Lellinger 2002), the proximal acroscopic lobes of basal pinnae shallowly pinnatifid to crenate (Fig. 1C), pinnule margins entire to somewhat crenate, sometimes slightly revolute (occasionally involute but possibly due to drying); adaxial surface green, not viscid-glandular, with sparse to moderately dense white farina

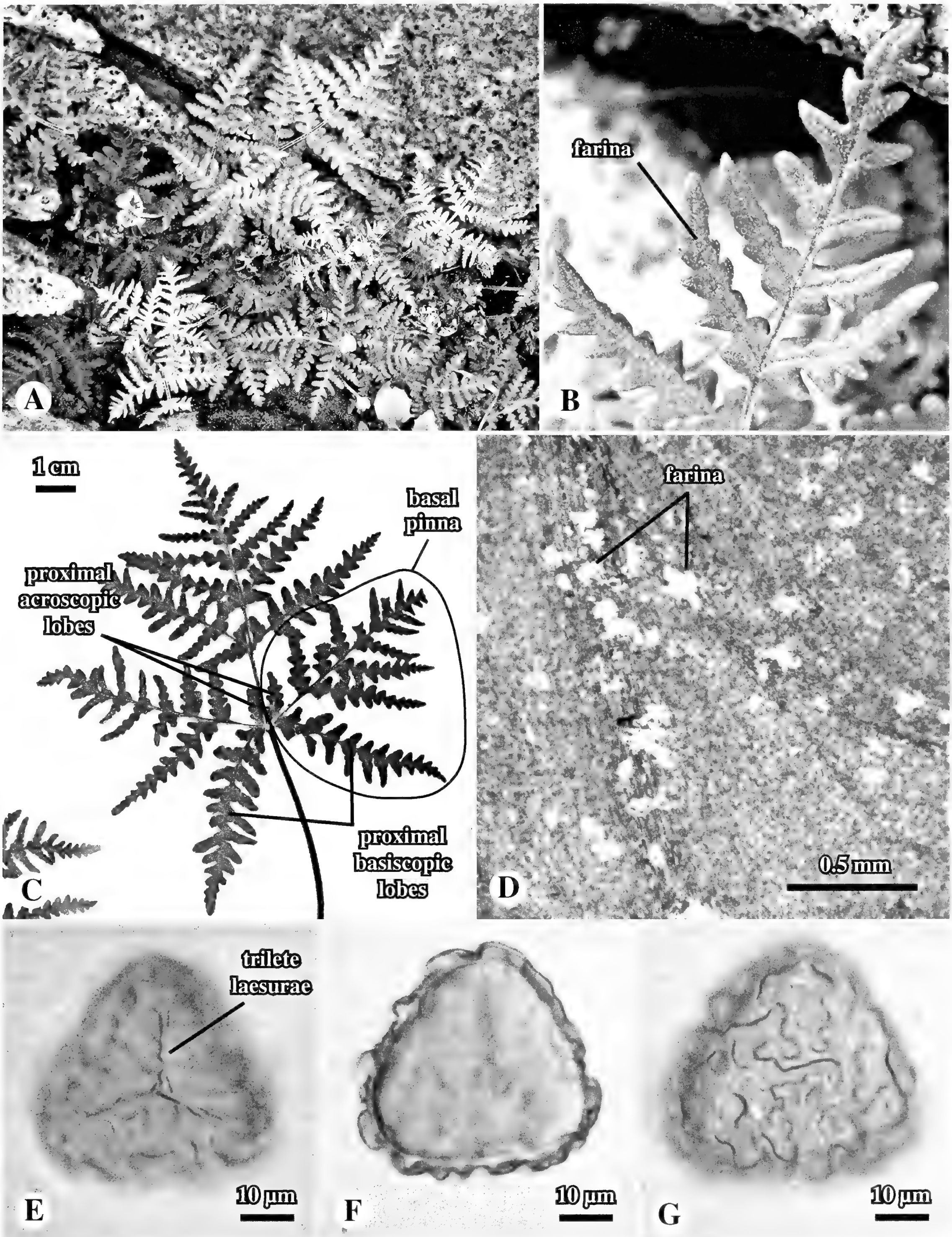

FIG. 1. A–B. *Pentagramma triangularis* subsp. *rebmanii*, growing in cracks of granitic boulders. Note scattered, adaxial farina. C. Blade of *P. t.* subsp. *rebmanii* (holotoype: SD 159328, *J. Rebman 11483 & G. Bustillos*), showing acroscopic and basiscopic pinnae. D. Close-up of adaxial surface of "C" showing farina. E–G. Differential interference contrast images of spore from holotype. E. Proximal surface, with trilete laesurae. F. Median optical section showing wall structure. G. Distal view showing merging tuberculate-rugulose sculpturing.

primarily along veins and rachis (Figs. 1B, D); abaxial surface moderately to densely white farinose. **Sporangia** 146–209 μm wide by 173–255 μm long, exindusiate; mature sporangium annulus dark amber. **Spores** 64 per sporangium, mean diameter per population examined 38.9–43.7 μm [absolute range 23.9–50.4 μm] tetrahedral, concolorous, tan, trilete, laesurae flush (Fig. 1E); wall sculpturing tuberculate-rugulose, with tubercles merging (Figs. 1F, G). Chromosome number unknown.

Distribution and Habitat. Native to a restricted geographical range of south-central to southeastern San Diego County, California, and inland, northwestern Baja California, Mexico, 33°02′ to 31°01′N, 116°44′ to 115°40′W. Occurring in chaparral, riparian-oak woodland, and desert transition communities on shaded slopes beneath rock outcrops with seasonal dripping water, in cracks and at the base of granite boulders, on granitic derived substrates of slope drainage streams, and on damp gabbro soils; elevation 450–1250 m; in association with *Cheilanthes clevelandii* D. C. Eaton, *Epipactis gigantea* Hooker and *Lilium humboldtii* Roezl and Leichtlin subsp. *ocellatum* (Kellogg) Thorne, *Pellaea mucronata* (D. C. Eaton) D. C. Eaton subsp. *mucronata*, *Pentagramma triangularis* subsp. *triangularis*, *Selaginella bigelovii* L. Underwood, and *Woodwardia fimbriata* Smith.

Phenology. Dependent upon winter rains to support both spore germination and new crozier growth from perennial rhizomes; sporangia mature in late winter and throughout the spring, persistent on completely desiccated specimens.

Etymology. This new subspecies is named in honor of Dr. Jon P. Rebman, Curator of Botany, San Diego Natural History Museum, who originally recognized that this subspecies differs from other *Pentagramma* taxa. Dr. Rebman is an outstanding taxonomist and an expert on the Cactaceae of Lower California and the flora of Southern California and Lower California. His extensive field studies of the flora of the Californias have resulted in the description of several new species from Baja California and Baja California Sur, Mexico.

Common Name. Rebman's Silverback Fern

Discussion

Pentagramma triangularis subsp. *rebmanii* is a new silverback fern currently known only from south-central to southeastern San Diego County, California and inland, northwestern Baja California, Mexico. It is similar to the other subspecies assigned to *P. t.* (Yatskievych et al. 1990) in having sharply bicolorous rhizome scales (Fig. 3A, B); terete, slender, glossy, red-brown stipes (Fig. 3E) with a single, V-shaped vascular bundle (Fig. 3D); blades with a strongly deltate-pentagonal shape and sessile to adnate pinnae (Fig. 1C); and spores that are uniformly tan, coarsely tuberculate with tubercles fused and appearing somewhat rugulose, lacking equatorial ridges (Figs. 1E–G). In addition, subspecies *rebmanii* has the abaxial, dense white farina typical of *P. t.* subspecies *maxonii* (Weatherby) Yatskievych, Windham, & E. Wollenweber, subspecies *viscosa* (Nuttall ex D. C. Eaton) Yatskievych, Windham, & E. Wollenweber (Weatherby 1920), and *semipallida* (Yatskievych and Windham 1993).

Pentagramma triangularis subsp. *rebmanii* generally has smaller mean spore diameter than other subspecies of *P. triangularis*. The range of the mean diameter for three different spore measurements from the holotype is 34.1–38.9 μm (total range of all spores measured for these three specimens equals 32.3–47.8 μm); the mean range of a total of seven specimens of subspecies *rebmanii*, including the three holotype measurements, was 38.9–43.7 μm (total range of all spores measured of these seven specimens equals 23.9–50.4 μm). This spore diameter overlaps only within the low values of the range for diploid populations of other *P. t.* taxa (Ault and Grant 1960; Smith et al. 1971). In contrast, tetraploids of other *P. t.* taxa had significantly larger spore diam. (Smith et al. 1971). A later study (Smith 1980) correlated farina flavonoid analysis with known cytological analysis (Table 1). Based upon spore measurements and flavonoid analysis, there appears to be no evidence for polyploidy in subsp. *rebmanii*.

Subspecies *rebmanii* differs from all other subspecies of *P. t.* in having scattered, white farina on the adaxial blade surface (Fig. 1B, D, 2E), and lightly scattered along the stipe (Fig. 3E). It further differs from subspecies *maxonii* in lacking the distinctive yellow capitate glands on the adaxial blade surface (Fig. 2A), and from *viscosa* in lacking the viscid-resinous adaxial blade surface (Fig. 2D) and entire margins on the distal and basiscopic lobes of the basal pinnae. The other two subspecies, *semipallida* (Fig. 2B) and *triangularis* (Fig. 2C), have a glabrous adaxial blade surface (Yatskievych and Windham 1993); subspecies *triangularis* has yellow abaxial farina, and subspecies *semipallida* has a thicker stipe, a more coriaceous dark green blade, and white abaxial farina. (Mickel and Smith 2004 treat subspecies *semipallida* as a synonym of subspecies *triangularis*.) A key to the taxa of *Pentagramma* occurring in California and Baja California, Mexico is provided below.

The new taxon is superficially similar to *Pentagramma pallida* (Weatherby) Yatskievych Windham, & E. Wollenweber in having farina on the adaxial blade surface (Fig. 2F, 3G). However, *P. pallida* differs in having a black, very glandular-farinose stipe throughout (Fig. 3H);

TABLE 1. *PENTAGRAMMA TRIANGULARIS* FLAVONOID AND CYTOLOGICAL ANALYSES. [1] Smith 1980, [2] Wollenweber personal communication, [3] Wollenweber & Dietz 1980, [4] Wollenweber & Smith 1981, [5] Wollenweber et al. 1979, [6] Inferred from spore measurements

Subspecies	Flavonoid analysis	Cytological analysis
maxonii	Major: Galangin[3]	Diploid[1]
rebmanii	Major: 2′,6′-dihydroxy-4′,4-dimethoxy dihydrochalcone[2]	Diploid[6]
	Minor: 2′,6′,4-trihydroxy,4′-methoxy-3′-methyl dihydrochalcone[2]	
	Trace: Kaempferol-4′-methyl ether[2] (on one of two specimens analyzed)	
semipallida	Major: Kaempferol 3,4′-dimethyl ether[1]	Diploid[1]
triangularis	Major: Ceroptin[4] (Holotype)	Diploid and Tetraploid[1]
	Galangin 7-methyl ether[1]	Tetraploid[1]
	Kaempferol[1]	Tetraploid[1]
	Kaempferol-4′-methyl ether[1]	Diploid[1]
	Kaempferol-4′ methyl ether and 7,4′-dimethyl ether[1]	Tetraploid[1]
viscosa	Major: 2′,6′,4-trihydroxy,4′-methoxy-3′-methyl dihydrochalcone[5]	Diploid[1]
	Minor: 2,′6′-dihdroxy-4′,4-dimethoxy dihydrochalcone[2]	

a more compact, less deltoid blade (Fig. 3G), and an adaxial blade surface that appears grayish due to the dense farina and associated, numerous globose glands (Fig. 2F, 3G). In contrast, *P. triangularis* subsp. *rebmanii* has a red-brown stipe (Fig. 3E) lightly scattered with white farina, a more open deltoid-pentagonal blade (Fig. 1C), and green adaxial surface (Fig. 3F) with scattered white farina (Figs. 1B, D, 2E).

Pentagramma triangularis subsp. *rebmanii* is found in a very narrow north-south range from a site in the Cleveland National Forest (SD 175764), San Diego County, California, approximately 52 km north of the U.S.-Mexico border to a site in northwestern Baja California (ASU 116042) and approximately 180 km south of the U.S.-Mexico border, and an east-west range of approximately 100 km between Bratton Valley (SD 175857) and the latter Baja California site (Fig. 4), the range approximately 12,000 km^2. This includes the dry inland foothill and mountain transition area between the coast and high Anza-Borrego Desert in San Diego County and the dry inland coastal scrub and foothills of northwestern Baja California that are so dependent upon the scarce winter rains to encourage growth of the native flora. Two of our San Diego County specimens are from locations completely burned during the 2003 Cedar fire; SD 157261 from chaparral and oak woodland on Viejas Mountain (growing with *Adenostoma fasciculatum* Hooker, *Epipactis gigantea*, *Lilium humboldtii* subsp. *ocellatum*, *Mimulus cardinalis* Bentham, *Platanus racemosa* Nuttall, *Quercus agrifolia* Nee, and *Woodwardia fimbriata*) and SD 175765 from chaparral on Poser Mountain (growing with *Adenostoma fasciculatum*, *Ceanothus oliganthus* Nuttall, *Cercocarpus betuloides* Torrey and A. Gray, *Heteromeles arbutifolia* (Lindley) Roemer, and *Mimulus clevelandii* Brandegee).

Farina flavonoid analyses indicate that *P. pallida*, a diploid species containing the C-methylated flavonones cryptostrobin, strobopinin, and desmethyoxymatteucinol (Wollenweber and Dietz 1980; Smith 1980), is quite distinct from *P. triangularis*. Further studies documented distinctive flavonoid patterns in each of the *P. triangularis* subspecies (Table 1). The major exudate component of subsp. *rebmanii*, 2′,6′-dihydroxy-4′,4-dimethoxy dihydrochalcone (Wollenweber personal communication), was previously reported (Wollenweber and Dietz 1980) as abundant on *Pityrogramma calomelanos*, *P. dealbata*, *P. tartarea*, and *P. trifoliata*; this same exudate was noted also as a trace constituent on a single population of *Pentagramma triangularis* var. *triangularis* [=*Pentagramma t.* subsp. *t.*] (Wollenweber et al. 1985) from northern California. The minor constituent in the farina of subsp. *rebmanii* is the same as the major flavonoid found in the exudate of *Pityrogramma triangularis* var. *viscosa* [=*Pentagramma t.* subsp. *v.*] (Wollenweber et al. 1979, Wollenweber personal communication) and vice versa. In addition, traces of kaempferol-4′-methyl ether (Wollenweber personal communication) were identified in one of two specimens of subsp. *rebmanii*; this compound was found also in some subspecies *triangularis* specimens that do not produce ceroptene (Smith 1980; Wollenweber et al. 1985). Thus, subsp. *rebmanii* exhibits only minor or trace similarities to the *P. t.* group. Interestingly, the new taxon is chemically more similar to species of *Pityrogramma* than to specimens of *Pentagramma triangularis* studied so far.

Pentagramma triangularis subsp. *rebmanii* is readily distinguishable in the field from the other subspecies by using a hand lens to observe the adaxial white farina, which appears as amorphous, mealy deposits (Figs. 1B, D).

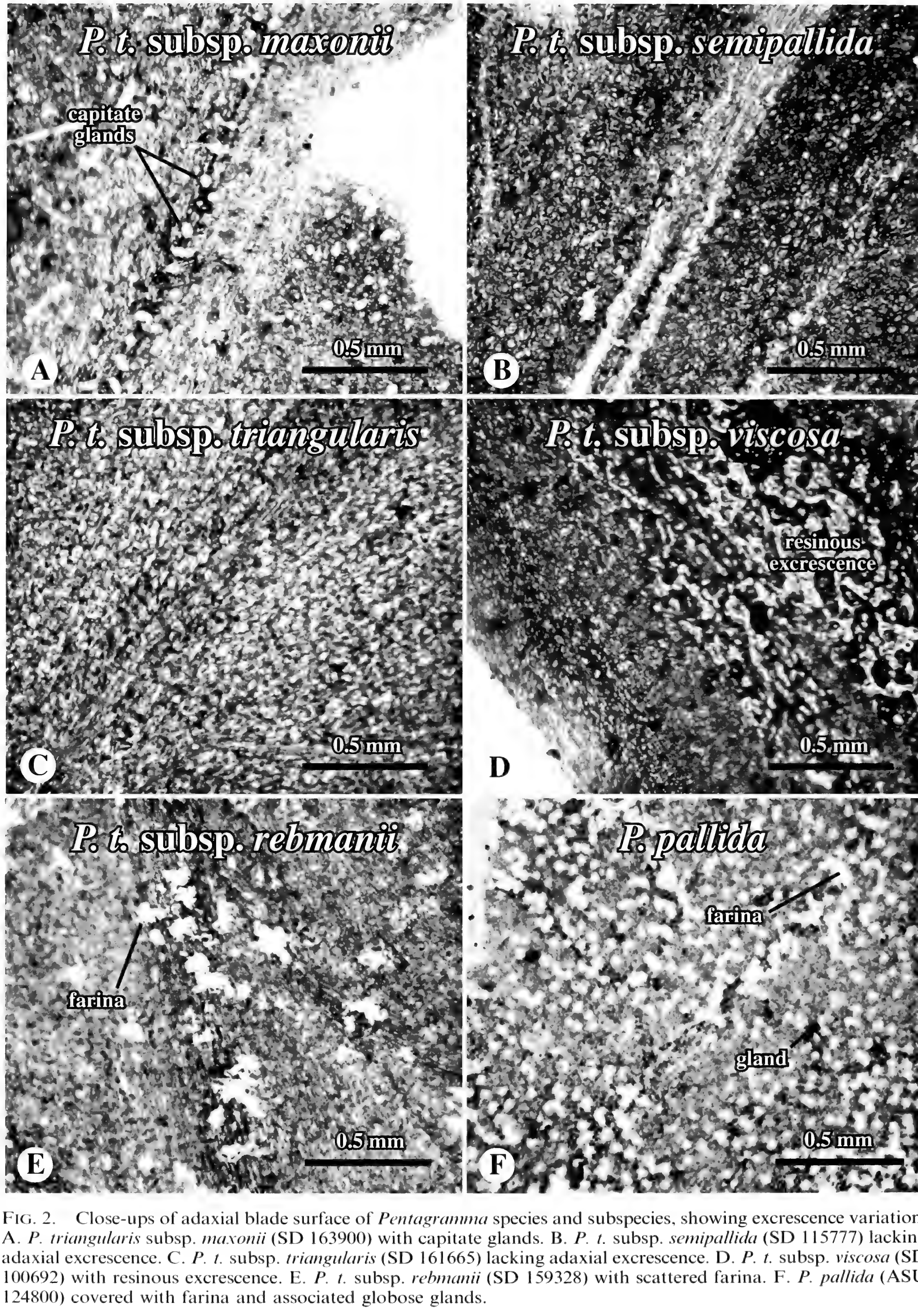

FIG. 2. Close-ups of adaxial blade surface of *Pentagramma* species and subspecies, showing excrescence variation. A. *P. triangularis* subsp. *maxonii* (SD 163900) with capitate glands. B. *P. t.* subsp. *semipallida* (SD 115777) lacking adaxial excrescence. C. *P. t.* subsp. *triangularis* (SD 161665) lacking adaxial excrescence. D. *P. t.* subsp. *viscosa* (SD 100692) with resinous excrescence. E. *P. t.* subsp. *rebmanii* (SD 159328) with scattered farina. F. *P. pallida* (ASU 124800) covered with farina and associated globose glands.

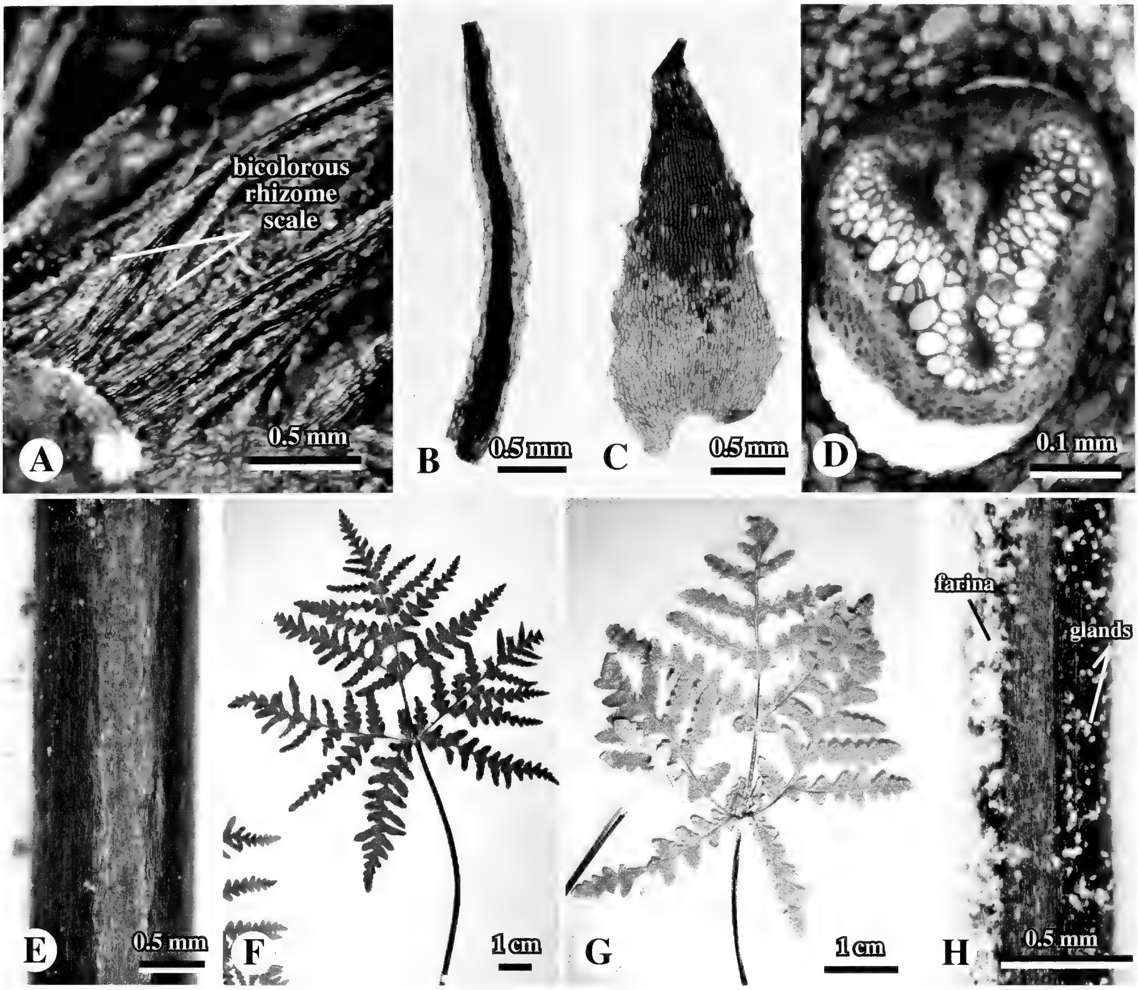

FIG. 3. A–F. *Pentagramma triangularis* subsp. *rebmanii* (holotype: SD 159328, *J. Rebman 11483 & G. Bustillos*). A–B. Rhizone scales, bicolorous and fibrillose. C. Clathrate scales from mid-stipe region with darkened apex. D. Stipe cross-section showing single vascular bundle (xylem V-shaped), adaxial side at top. E. Stipe surface, glossy red-brown with sparse farina, at mid-region. F. Blade, adaxial surface with scattered farina. G–H. *P. pallida* (ASU 124800). G. Blade adaxial surface covered with farina and associated globose glands. H. Stipe surface, dull blackish with glandular-farinaceous deposits, at mid-region.

KEY TO THE *PENTAGRAMMA* TAXA OF CALIFORNIA AND BAJA CALIFORNIA, MEXICO

1. Blade adaxial and abaxial surfaces white farinose
   2. Stipe dull purplish-black to black, with moderately dense, grayish-white farina along entire stipe length; blade adaxial surface with overall grayish appearance . . . . *Pentagramma pallida*
   2′. Stipe glossy red-brown aging dull, dark red-brown, with lightly scattered white farina; blade adaxial surface green . . . . *Pentagramma triangularis* subsp. *rebmanii*

1′. Blade adaxial surface viscid-resinous, glabrous, or with scattered yellow capitate glands; abaxial surface white or yellow farinose
   3. Blade adaxial surface viscid-resinous, distal pinnae and proximal basiscopic lobes of basal pinnae mostly entire . . . . *Pentagramma triangularis* subsp. *viscosa*
   3′. Blade adaxial surface glabrous, or with scattered yellow capitate glands, distal pinnae and proximal basiscopic lobes of basal pinnae deeply pinnate-pinnatifid
      4. Blade adaxial surface with scattered yellow capitate glands. . *Pentagramma triangularis* subsp. *maxonii*
      4′. Blade adaxial surface glabrous
         5. Blade abaxial surface white farinose . . . . *Pentagramma triangularis* subsp. *semipallida*
         5′. Blade abaxial surface yellow farinose . . . . *Pentagramma triangularis* subsp. *triangularis*

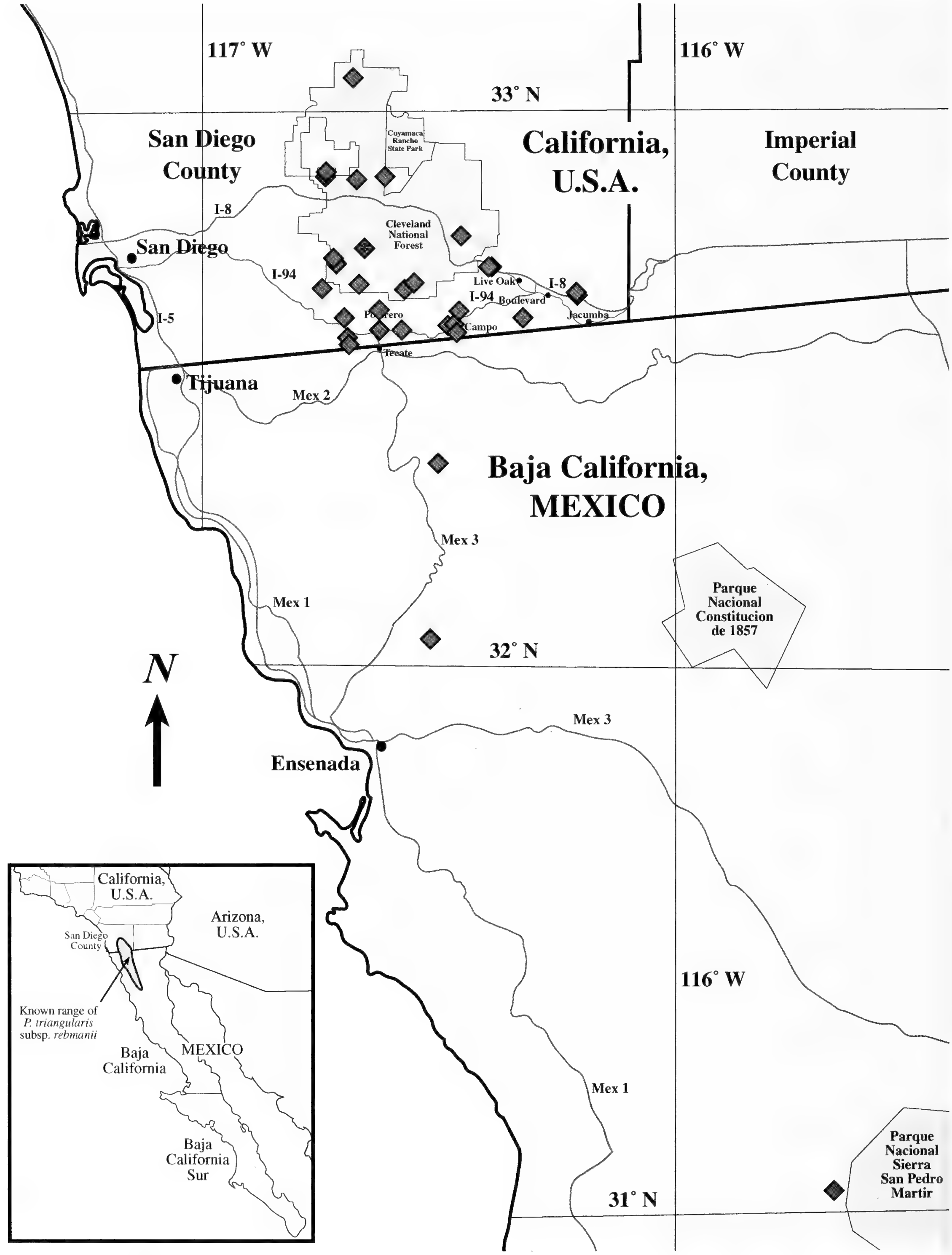

FIG. 4. Localities for collections of *Pentagramma triangularis* subsp. *rebmanii*, to date known only from south-central to southeastern San Diego County, California, USA, and inland, northwestern Baja California, Mexico. *=holotype locality.

Acknowledgments

We would like to express our gratitude to Dr. Jon Rebman for initially pointing out the distinctiveness of this new subspecies and to Jeannie Gregory for photographs shown in Figs. 1A, B. We thank Dr. George Yatskievych for encouraging study of this new taxon and Dr. Eckhard Wollenweber for farina analysis. We express our appreciation to Dr. Exequiel Ezcurra and Krista Pelayo for Spanish translation; and to Ruth Kirkpatrick, John Hunter, and two anonymous reviewers for their constructive critique of this manuscript. We thank ASU, CAS-DS, RSA-POM, UC-JEPS, and US herbaria for *Pentagramma* specimen loans.

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MADROÑO, Vol. 54, No. 4, pp. 354–365, 2007

REVIEWS

Fire in California's Ecosystems. Edited by NEIL G. SUGIHARA, JAN W. VAN WAGTENDONK, KEVIN E. SHAFFER, JOANN FITES KAUFMAN and ANDREA E. THODE. University of California Press. Berkeley, CA. 612 pp. $75.00. ISBN-13 948-0-520-24605-8.

Plant biologists in California have long-recognized the important effects of fire on the state's vegetation and flora (e.g., Brandegee 1891), and will appreciate a book covering this topic. We are, however, only one of the audiences for this new book. Interest in fire has proliferated across disciplines, and in policy and management arenas. It is difficult to capture a topic as multi-disciplinary and complex as fire in California ecosystems and the management issues it creates, even in a large book such as this. Yet the book does aim to be a complete reference on these subjects. The authors and editors are to be commended for putting together a large volume of information in pursuit of an ambitious goal, and producing an attractive, well-illustrated textbook. This book has many voices: five editor/authors and 45 total authors. Most (24) are from large land management agencies, primarily the U.S. Forest Service. The book is dedicated to Harold Biswell, best known for his devotion to managing wildlands using fire.

Fire in California's Ecosystems is divided into three sections. The first is an introduction to fire ecology. The second describes fire history and ecology in nine bioregions in California. The third section is about fire management. The book includes a short glossary. (This glossary does not include some undefined terms used in the book that are technical [e.g., pyrolysis], or potentially ambiguous [wildland-urban interface].) There is also a useful appendix with an explanation of plant alliances and species characterizing California's bioregions. Special topics are included as short, but interesting sidebars throughout the book. Below, I critically evaluate material from each section most relevant to plant biology for completeness, accuracy and consistency.

Section I: Introduction to Fire Ecology—There are chapters on fire as a physical process, how fire is affected by weather and climate, and how soil, water, air, plants, and animals are affected by fire. These chapters provide the reader with a primer on fire behavior and ecology. Chapters vary in their level of detail, with the one on fire and animal interactions being longest. The chapter on fire as a physical process is an informative summary of an often poorly understood topic. For example, it is often presumed that fire spread is governed by fuel load, but this chapter explains how rate of fire spread and fuel load tend to be inversely correlated because fuel and biomass are heat sinks and can decrease wind. The subject of fire behavior could have been more detailed, however, to allow better explanation of some concepts, for example that ladder fuels "allow" a fire to reach the canopy of a forest. If overstory tree crowns are sufficiently heated from below (a function of windspeed and interrelated surface fire intensity) they can easily bridge a considerable fuel gap and burst into flame. This is not clear, and the reader may conclude incorrectly from the description of canopy fuels that fire must climb a hypothetical ladder to effect crown fire. There is also ambiguity about foliage density needed to propagate fire vertically (which will depend on its chemical energy) and whether shrubs are ladders (apparently no in Section I and yes in Section III). Thus, it is not clear what constitutes a "ladder" fuel. In addition, crown fire requirements are supposed to be modeled based on live foliage, not other canopy biomass, an important distinction (Cruz et al. 2004) that is not conveyed. To explain crown fire initiation, the first phase of combustion, preheating and the thermal degradation (pyrolysis) of solid fuel to the gaseous phase, could have been examined more with respect to chemical properties and energy content of foliage that support ready ignition of tree and shrub crowns exposed to heat (e.g., waxes, oils, and volatiles that vaporize at low temperatures).

I was surprised to read in the first section that the editors do not recognize fire as an ecological disturbance. The ecological literature defines any event that causes sudden mortality or a reduction in biomass, as well as an increase in resource availability, as a disturbance. Fire is a classic natural disturbance. The basis for understanding vegetation change and secondary succession is the character of disturbances, and the legacies left behind, such as surviving organisms, seeds, spores, soil, dead trees, logs, and other biomass (White and Jentsch 2001). Natural disturbances are vital to biodiversity (Petraitis et al. 1989), and their effects in disrupting equilibrium and competitive exclusion and in creating spatial and temporal environmental heterogeneity, are key for understanding the complexity of nature. In addition, a key for understanding when degradation of natural systems will occur is the occurrence of novel or compounded disturbances (Paine et al. 1998). By describing fire as distinct from disturbance, the reader may be directed

away from one of the most important, extensively studied topics in ecology that provides a foundation to understand the effects of both fire and fire management disturbances.

Additional problems in the introductory section include a table on plant adaptations that appears to indicate that *Ceanothus megacarpus* is serotinous, an extreme fire-specialization where seeds are stored in fruiting structures that open to release them after being heated by fire. This would be quite significant if true because only gymnosperms are serotinous in the Northern Hemisphere. The introductory section also mentions that serotiny occurs in lodgepole pine in California. However, this applies only to the subspecies of lodgepole found in the Rocky Mountains, unless there has been a new discovery (no citation is given). Chamise chaparral is used as an example of a community with very low post-fire plant diversity, but this is an especially poor choice because chaparral dominated by chamise can be very diverse after fire, as described in Section II. Similarly, a section on spatial patterns of fire severity uses chamise chaparral as an example of where fire severity will be homogeneous, but this chaparral has been found to have pronounced local gradients and spatial complexity in fire effects as described elsewhere in Section I. However, the strong patterns are not caused by dead branches on the ground as described, but the collapse of live shrub crowns during fire. Finally, a sidebar describes fire in southern California chaparral as a strongly age-dependent process, but does not refer to literature presented in Section II illustrating that fires have instead been found to sweep through young and old stands with similar probability. As with other cases where the book presents conflicting information in different sections, there is not an attempt to reconcile or cross reference competing treatments so that the reader may be aware of them.

Section II: The History and Ecology of Fire in California's Bioregions—There are separate chapters on each of the nine bioregions into which California is divided. These chapters provide nice summaries on the climate and geography of the bioregions. There are also overviews on the historic occurrence of fire, separated into presettlement (prehistoric), post-settlement (historic), and current time periods. This illustrates how fire regimes have changed continuously in the past due to climatic and cultural influences. Interactions between fire regime and plant communities are described separately for ecological zones within each bioregion. Plant biologists in particular will want to refer to the informative appendix listing plant alliances and species characterizing ecological zones within each bioregion. In some chapters, there are sections on fire-specialized vegetation, such as serotinous

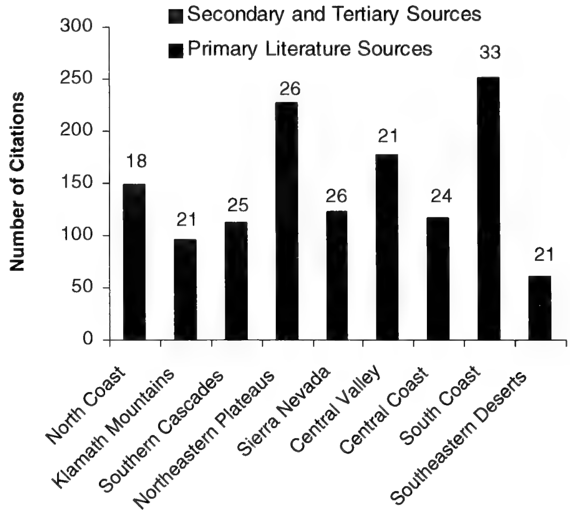

FIG. 1. Primary and secondary and tertiary information sources cited in bioregional chapters of *Fire in California's Ecosystems*. The numbers above the bars are the pages of narrative in each chapter.

pines, which are particularly interesting. Each bioregional chapter concludes with a section on management issues. Management is also addressed in most of Section III. It would have been more efficient to locate all the management text together there. This would have helped reduce inconsistencies described below, and allowed for more complete coverage of other topics by bioregion.

To help compare completeness of regional treatments, I charted the number of primary and other literature citations in each chapter in Section II (Fig. 1). The large disparity in citations in part reflects differences in the amount of research conducted in different regions. For example, comparatively little research on fire has been done in the Mojave and Sonoran Desert regions of California, where fire was very rare prior to the recent spread of exotic grasses. In the South and Central Coast bioregions, there has been relatively little fire history work to cite. Conversely, numerous studies on fire history are cited in chapters on forested bioregions. These chapters could have been more complete by discussing and citing more ecological literature. Interesting research could have been cited in many of these chapters on subjects such as the reproduction of non-serotinous conifers following crown fires and survival of seeds in their cones, postfire growth and dynamics of these conifers and how this can be facilitated by mycorrhizal fungi shared with *Arctostaphylos* and *Arbutus*, fire severity patterns in conifer forests, and fire and forest disease and insect interactions. In addition, there are non-forest vegetation types that are widespread, but not mentioned in some bioregions, such as chaparral

in the North Coast bioregion. This is being replaced by Douglas-fir in the absence of fire. This is a key biodiversity concern on National Park lands.

Also omitted is any explanation or citation of literature on the limitations of fire scar methods for describing fire regimes. Existing literature describes how opportunistic sampling and data aggregation, can significantly underestimate the spatial and temporal variability in fire that occurred across landscapes in recent centuries. This subject is noted in the climate and weather chapter in Section I, which explains how a fundamental property of all fire regimes is that large fires account for the majority of cumulative area burned, but fire scars provide mainly a record of fires in the past that spread very little before going out. This is not only a problem for estimating past fire size, but also behavior, because large fires often burn under conditions ranging from extreme to very mild. The omission of key literature for understanding past fire regimes in California is not consistent with the intent of the book to be a complete reference.

Section III: Fire Management Issues in California—There are 8 chapters addressing topics ranging from Native American fire use, to current fire management, and effects of fire on air resources. There are also chapters on fire and exotic and at-risk species. Much interesting information is summarized. However, there are also notable omissions, and areas of inconsistency with other portions of the book. Most of these are in the chapter on current fire and fuel management. This subject has important implications for vegetation and flora, and thus will be the focus here.

In contrast with earlier portions of the book describing wildfire as a vital ecosystem process, it is viewed mainly as a destructive agent in the assessment of current management. Given the history of homes burning in wildfires in California, it is understandable for managers to view fire in this light. However, the loss of homes in California can also be recognized as a planning problem (Halsey 2005), and a particularly relevant omission in a book covering fire management issues in California is the literature on the cause of home ignitions during wildfires and how to prevent them. This subject is not as intuitive as it may seem. As described in a number of publications by structure ignition specialist, Jack Cohen, who has investigated the cause of home loss associated with wildfires throughout the western United States, these ignitions can occur during low intensity ground fires, without the vegetation adjacent to the home burning, and well inside the perimeter of communities, not just at the urban interface. A primary cause of ignitions is long-distance embers. Even where wildfire extent has already been reduced to historic lows by fire suppression, home ignitions are increasing. Wildlands will continue to burn and produce long-distance embers regardless of management. The only way home ignitions can be effectively eliminated is by treating the home and its immediate surroundings (Cohen 2000). This is an important lesson that managers and policy makers still fail to grasp, which the book could have addressed. An unfortunate consequence of current management approaches that continue to look to fire prevention in wildlands to protect homes has been complacency about fire planning and incentive for more unsafe development in fire prone ecosystems (Kennedy 2006). The pressure for such development and the need to justify enormous fire prevention expenditures in turn creates incentives to promote the viability of fire prevention approaches in wildlands. Fire behavior may then tend to be viewed too much as a function of management, especially effects of fire prevention, instead of climate, weather and topography. In chaparral, assumptions that fire is preventable and not largely weather-driven are especially unrealistic, as described in Section II but not in the management section. The treatment of current fire management issues does not take a hard look at the potential effectiveness of treatments in wildlands, nor explain the need to make the specific actions that will prevent home ignition, the first and foremost management priority.

Ironically, the justification presented for continuing to invest limited resources heavily in fire prevention approaches in wildlands is that this is needed to combat uncharacteristically large and severe fires caused by the effects of… fire prevention. However, where most of the state's largest fires are occurring, in southern California chaparral, fire prevention has not been successful. Instead, the opposite situation, more frequent fire, has been occurring. This is due largely to human ignitions and grass invasion, as explained in Section II. Moreover, large fires have always characterized this vegetation, and the probability of these has not changed. Conversely, where fire has been prevented, in forested regions, as described in Section II, this has not lead to an increasing trend in wildfire activity (Fig. 2). Section II explains how current rates of burning are a fraction of those in the past, when fires were not only frequent, but also included a range of severity. In addition, chaparral has been replaced by forests, which support much less crown fire. Thus, both amounts of fire and area affected by high severity fire appear to have been decreased overall where fire prevention has been effective. Where fire severity has been increased, this may be traced to the effects of silvicutural activities (Weatherspoon and Skinner 1995).

The chapter on current management, in explaining the case for large investments in

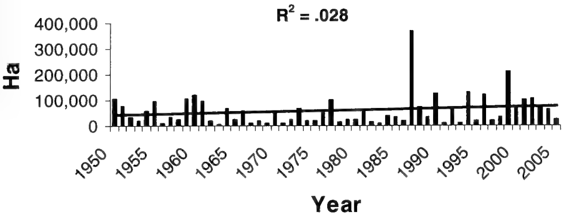

FIG. 2. Annual area burned from 1950 to 2005 in bioregions of northern California in which fire occurs predominantly in forest. Bioregions are the Bay Area, Klamath, Modoc (includes S. Cascades), and Sierra Nevada. Bioregions and fire perimeter data from the California Department of Forestry and Fire Protection, available with metadata at: http://frap.cdf.ca.gov/index.htm.

wildlands treatments to combat an emergency due to effects of fire prevention, equates fuel with biomass. As defined in the glossary and Chapter I, however, fuel is specifically the biomass that feeds combustion. Forest biomass increases as trees grow, but commonly stabilizes. So do the fuels that influence fire behavior: ground, and especially foliar fuel. Equilibrium fuel depths in California forest floors were previously described in California forests by renowned soil scientist Hans Jenny and others at Berkeley (e.g., Kittredge 1955). Although the chapter on current management says that fuel is accumulating "far beyond natural levels," a sidebar presents conflicting data showing surface fuel approaching, after only 10 yr following fire, levels that occurred with over a century of fire exclusion. In terms of foliage amounts, ecophysiological literature describes how a proxy for this, leaf area, also reaches a maximum in forests early in succession. Fire severity can also decrease with increasing biomass as forests replace chaparral, as they have in many areas. While biomass today may exceed "natural" levels the potential for vegetation to burn has always been high. What is clearly different today are extensive urban and intermix fuels prone to ignition.

Emergency fire management that is based on "preventing fire and reducing its effects" by treating biomass in wildlands, the focus of the management chapter, can be counter to safety and restoration needs. Investing heavily in fire prevention and extensive treatments in wildlands can divert limited resources and attention away from the highest safety priority, the home ignition zone. The massive expenditures for fire prevention efforts and incentives to continue them and promote their effectiveness can indirectly subsidize poor planning that undermines safety (Kennedy 2006). Where restoration is needed due to lack of fire, preventing fire increases the problems created by fire prevention. Thinning or other partial harvesting and mastication places biomass on the ground, where it is converted to fuel, increasing potential fire effects. The resulting increased solar radiation and decreased wind resistance due to tree removal can promote more rapid spread and intensity of wildfires, as described in Section I. Although these mechanical treatments and grazing are referred to as restoration in the chapter on current management, they do not have the unique effects of fire described in Sections I and II that are needed for restoration. The treatments have the additional drawback of introducing novel and compounded disturbances and exotic species. However, while fire itself is needed for restoration in many areas, the recommendation to expand prescribed burning programs in chaparral is not a logical response to a problem of excess fire and could work against restoration by causing further grass invasion. Grazing treatments in chaparral and desert regions may also increase non-native grasses that cause excess fire there.

Where fire has been excluded, only treatments involving fire can be effective at both reducing available fuel and restoring fire. However, due to safety and air quality concerns, as described in Section III, prescribed burning is far too limited in extent to return past amounts of fire. Moreover, even prescribed fire may not effectively reduce fuel or replicate past fire if too subdued, small in area, or if done during the off-season, when effects on fuel, soils, breeding species and exotics may be undesirable. Where thinning or mastication slash is burned, effects on soils and atmospheric emissions can be increased. Ironically, the large fires that are considered disasters from a management perspective avoid these concerns and accomplish most fuel reduction and ecological restoration where fire is needed. However, if fire and its beneficial effects are to be truly accomodated and restored where they have been excluded, a strategy that prioritizes specific actions required to prevent home ignitions is needed.

Although a considerable part of the book is devoted to management issues, there are a number that are overlooked in Section III. An assessment of the practice of "salvage logging," perhaps the most controversial fire management practice today, is a particularly noteworthy omission, especially considering recent literature on the subject. Although managers cite restoration and fuel reduction goals in promoting this treatment, large quantities of biomass are relocated to the ground and converted to fuel, and reproduction by conifers and other species is inhibited. There are also concerns over the need to protect rather than cut burned forest habitat, which supports unique species assemblages and vegetation renewal processes. This habitat has become rare with fire exclusion. The effects of a controversial management practice, post-fire seeding, are nicely described in a separate sidebar

in the chapter on fire and aquatic and watershed resources. This example could have been followed in describing collateral damage from commercial logging and grazing treatments done in the name of fire managment.

CONCLUSIONS

The topic of fire in California ecosystems is complex and multidisciplinary, and very difficult to encompass in one book. *Fire in California's Ecosystems* summarizes well much of the relevant literature. However, there are important topics that are omitted or not adequately addressed with up-to-date perspectives. Other literature can fill these gaps. Bond and van Wilgen's 1996 short classic, *Fire and Plants*, better addresses fire as an ecological and evolutionary force and recognize it as a natural disturbance process. These are important perspectives for understanding fire, particularly as it affects plant biology and biodiversity. Perspectives that do not shy away from critically analyzing existing land management and planning, and that more broadly consider solutions to today's wildfire problems are also important to consider. In addition to the aforementioned books by Halsey (2005) and Kennedy (2006), a good accompaniment to *Fire in California's Ecosystems* is the recently published book *Wildfire: a Century of Failed Forest Policy*, edited by Wuerthner (2006). As these books point out, incentives created by huge fire budgets and commercial activities discourage pursuit of specific actions needed for protecting human communities from fire and restoring fire regimes in plant communities. These are particularly important needs in California.

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Fire in California's Ecosystems. Edited by NEIL G. SUGIHARA, JAN W. VAN WAGTENDONK, KEVIN E. SHAFFER, JOANN FITES KAUFMAN and ANDREA E. THODE. University of California Press. Berkeley, CA. 612 pp. $75.00. ISBN-13 948-0-520-24605-8.

CALIFORNIA'S FIRE ECOLOGY: A NEW SYNTHESIS

In the foreword to *Fire in California's Ecosystems* Jim Agee predicts: "The volume you hold now will become the secular bible of fire ecology for Californians." Dr. Agee's statement implies that the reader need look no further to satisfy his/her questions regarding ecology and management of fire in the nation's third-largest state. *Fire in California's Ecosystems* is a comprehensive synthesis of the current state of knowledge for fire ecology and management in California's diverse ecosystems.

The book is organized in three parts, including a first section on basic fire ecology, followed by a collection of chapters describing fire ecology and management for each of nine bioregions, culminating in a collection of eight chapters geared towards over-arching fire management issues. *Fire in California's Ecosystems* is very well put together for a collection of contributed chapters. The editing is polished and the authors have followed a common organizational template. Sidebars are generally very useful and cover topical features such as fire climate, landscape dynamics of chaparral communities, plant adaptations to fire, and exotic annual grasses, to name only a few. Illustrations and GIS maps are clear, consistent among chapters, and professionally formatted. Copies and scans of many of these illustrations are sure to appear

in numerous lectures on fire ecology and forest management.

The first seven chapters would be valuable reading for any fire ecology course, anywhere in the world. Each of these chapters is clear and comprehensive. Taken together they provide a solid overview of fire as an ecological disturbance. Chapters cover the basic concepts of fire ecology with regard to weather and climate, fire physics, fire regimes and plant community dynamics, fire effects on the environment, fire effects on plants, and fire effects on animals. Unfortunately, the coverage of ecosystem effects of fire is relatively limited. The "physical environment" effects of fire (soil, water, air) are covered in just one chapter (Chapter 5). This chapter is well-presented, but this is a huge area of study and the book might have been better served as a core fire ecology text if the air, soil and biogeochemistry, and water effects had been broken out into separate chapters. Also, this chapter omits discussion of fire regime change (e.g., fire exclusion effects). Chapter 6 on *Fire and Plant Interactions*, contributed by Joann Fites-Kaufman and coauthors, includes an informative discussion of plant adaptations and fire effects across several levels of ecological organization. Jon Keeley has contributed a thoughtful sidebar on the evolution of fire adaptations.

The nine bioregional chapters (Part II of the book) are organized consistently according to subdivisions of ecological zones, and vegetation alliances within ecological zones. Each of these chapters includes a general description of the physical environment, an overview of fire history, a description of major ecological zones including fire ecology and interactions between the fire regime and plant communities, and contemporary management issues. Included in each chapter are tables summarizing life history adaptations to fire for key plant species within each bioregion, as well as summary tables describing fire regime parameters (fire seasonality, return interval, extent, severity, etc.) for each vegetation type. Such organizational consistency is impressive and doubtless reflects strong-willed editorship as well as substantial commitment on the part of the authors. A high level of organization is needed to create a coherent picture of such diverse fire environments and ecological systems as are contained within the political boundaries of California, which includes the highest and lowest elevations of the lower 48 states.

Most of the regional chapters are written by scientists with considerable local experience in their assigned ecoregion, and many excellent narratives are included in the book. The Klamath Mountains chapter (by Carl Skinner) provides a well-honed discussion of how fire behavior and fire regime have interacted with the physical landscape template, with respect to the distinctly convoluted topography and famously complex geology of those particular mountains. The Northeastern Plateaus chapter (by Gregg Riegel), describing California's portion of the Great Basin, includes a nuanced description of fire ecology in the sagebrush steppe zone. There are useful discussions of interactions among fire regime, plant community succession, and directional vegetation shifts such as have been prevalent in the western United States over the past century. Many of the regional chapters, and especially the Sierra Nevada chapter (by Jan van Wagtendonk), contribute discussions of historical human influences including those prior to Euro-American settlement, and place current fire and forest management issues within this long-term context. A recurring theme of the regional chapters is the importance of fire exclusion for altering contemporary fire regime and ecological processes. As stated in the Sierra Nevada bioregional chapter (p. 290), "The question becomes how to restore natural fire regimes without adversely affecting at-risk species and their habitats… These species evolved with fire and the answer must include fire." However, bioregions that are characterized by chaparral vegetation at lower elevations (South Coast, portions of the Central Coast) now experience more frequent fires than historically, as a result of human ignitions and urbanization.

Several of the bioregional chapters (North Coast, Southern Cascades, Central Valley) paint a picture of Native American burning that, while quite plausible, is supported by a paucity of primary literature sources. The strength of evidence supporting native burning could be presented in a less anecdotal fashion, and the authors could have made clearer that while aboriginal fire may have been critical for shaping vegetation structure in certain vegetation types, it was likely of low importance for other types, such as those in less productive, high-elevation areas.

The final section of the book (Chapters 17–24) addresses fire management issues that range from the over-arching to the very practical. The important questions are not neglected. How can we describe a historic range of variability, or meaningful reference conditions for restoration, in the context of Native American fire use? How can we incorporate fire use in our management planning and still protect people and their resources given the great increases in population over the past decades? These chapters emphasize fire effects and discuss the negative effects of fire use that can occur with less than perfect planning, with respect to aquatic systems, air quality, exotic plant invasions, and habitat for at-risk species.

Chapter 17, contributed by Kat Anderson, presents an exhaustive yet balanced description of Native American fire use. The chapter describes the continuum of influences across this

large and heterogeneous state, including areas of low influence due to low population (serpentine and subalpine environments) as well as areas where Native American fire management was likely high because of high population densities and cultural fire use (northwest coastal prairies region).

In Chapter 18, Scott Stephens and Neil Sugihara provide a thorough background into the historical events and cultural influences leading to the triumph of fire suppression policies over a "light burning" paradigm for forestry in the western U.S. The discussion eventually winds its way to contemporary fire management including new manifestations of the fire use paradigm, leading to today's changing perspectives and policy shifts. Husari et al. (Chapter 19) continue with this theme in their chapter on fire and fuel management, describing the shift in management focus and policy from fire control to fuel management. As for most of the other chapters in this book, there is a laudable effort to place where we are today in the context of past management practices and historical influences.

Chapters 20–23 describe fire management issues regarding aquatic resources, air quality, invasive plant species and species of conservation concern. The first of these chapters (watershed resources, contributed by Andrea Thode and others) is brief but well-focused, and performs the amazing feat of not repeating material from earlier chapters. There are useful summary tables contrasting various watershed rehabilitation methods. Fire is treated as an integral watershed process and there is a balanced discussion of controversial ideas pertaining to active management of forested riparian zones. There is useful emphasis on linking watershed restoration and fire management activities. The air quality chapter (by Suraj Ahuja) provides an informative summary of fire effects on air quality and how fire and fuels management are constrained by air quality regulations. The invasive plant species chapter (by Robert Klinger) elucidates the complex, two-way interactions between fire regime and exotic plants. Missing from this chapter is mention of the interaction between fire and invasive forest pathogens such as Sudden Oak Death.

It is unfortunate that the management section of the book lacks a chapter on wildland fire use in undeveloped areas. Over 14 million acres in California are managed as wilderness and how to manage wildland fire in these areas has become an issue of prime importance. The management section chapters instead focus almost exclusively on issues of the wildland-urban interface and active forest and fire management in traditionally managed forests.

Neil Sugihara takes the lead in summarizing all three sections of the book (Chapter 24). This final chapter is essentially a call for society to act now to restore fire as an ecosystem process, even when knowledge is incomplete and ecosystem alterations and discontinuities prevent a return to historical conditions. We need to manage fuels and fire regimes so as to counter the ecosystem changes and negative biodiversity effects resulting from a century of fire exclusion. However, certain bioregions and vegetation zones (coastal chaparral, subalpine forests) have not experienced fire exclusion and need to be managed differently, as pointed out by Jon Keeley in his South Coast chapter. Coastal chaparral now burns more frequently and later in the year than prior to settlement, but the actual area burned is within a historic range of variability because suppression efforts keep most fires small. Fire management and landscape restoration must be adapted to the particular bioregional setting, and this book provides the regionally specific information required to support such efforts.

The book's emphasis on providing a compendium of the current state of knowledge regarding California fire ecology can be seen as a limitation as well as a strength, in that it summarizes what we know rather than suggests directions for future research. Some of the chapters could have been reined in a little more with respect to repetitive, extraneous detail. The book has been closely edited for consistency in organization, but not necessarily for content and brevity. *Fire in California's Ecosystems* is not intended to be read cover to cover, but rather will serve as a reference work. The persistent reader will emerge with new information and perspectives gained from diverse scientists and forest managers who have spent considerable portions of their careers working with the topics and geographic areas about which they have written.

This comprehensive, multifaceted work will be informative for fire scientists and managers at all levels. It interweaves biological, physical, cultural and operational aspects of fire science through a collection of contributed chapters. The usefulness of the work clearly transcends the state of California. *Fire in California's Ecosystems* is one of the more valuable fire ecology books to come out in a long time, and it has something to offer nearly everyone: research scientists and university instructors, fire and forest managers, students of various ecological, environmental and natural resource disciplines, and the interested citizen. It may not make for good "light reading" at the beach, but is a resource worth having on your bookshelf.

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Weeds of California and Other Western States. By JOSEPH M. DITOMASO and EVELYN A. HEALY. 2007. University of California Agriculture and Natural Resources Publication 3488, 6701 San Pablo Avenue, Oakland, CA 94608-1239. Two volumes, 1808 pp. plus CD with photographs Softcover. $100.00. ISBN 1-879906-69-4.

In California, this may be the most important book since the publication of *The Jepson Manual* in 1993. There are three compelling reasons for this. First, unlike several local floras that have been published in the meantime, this treatment covers the whole state of California. Second, because California is one of the three U.S. states with the highest number of naturalized plant species, and because a substantial proportion of weeds are naturalized species, this component of the flora deserves a special attention. Third, the last comprehensive book on weeds of California was published 56 yr ago (Robbins et al. 1951; actually, 66 yr ago, because the 1951 edition was only minor modification of the first edition from 1941).

Weeds of California (Robbins et al. 1951) covered 693 species, 437 (63%) non-native and 256 (37%) native. Based on my counting, the main text of the DiTomaso and Healy's volumes deals with 677 (83%) non-native and ca. 140 (17%) native weedy species. Moreover, 714 additional, rarely naturalized or casual non-native species are listed in the Appendix. Out of ca. 817 species treated in the main text, 737 are illustrated by at least one color photograph, most of them by several photos of mature plants, seeds, and seedlings. There is probably no other country in the world with a so well illustrated weed manual. Plant identification is facilitated by tables summarizing important characters of species within genera or groups of closely related genera (e.g., ice plants and relatives, *Amaranthus*, *Bidens*, *Brassica* + *Hirschfeldia* + *Sinapis*, *Centaurea*, *Euphorbia*, etc.). Thirteen shortcut identification tables for groups that share similar, unusual, or relatively uncommon characters (plants with prickles, spines, or thorns, plants with palmately compound leaves, plants with square stems, etc.) are also quite helpful. Moreover, two grass identification keys are provided: a key based on all characters and a key based on vegetative characters only. The main body of the volumes contains weed descriptions that are presented in alphabetic order according to family, genus, and species. The text includes not only detailed morphological descriptions of the taxa, but also information on distribution, habitat, reproduction, phenology, and management options. All morphological terms used in the text are explained in an illustrated glossary.

Regarding the main text and illustrations, I have only a very few comments. Among over 2000 photographs, I found only one mistake: the photograph of *Trifolium angustifolium* on p. 811 is definitely not a picture of this species, but of a different clover. *Polycarpum* (pp. 573–575) should be spelled *Polycarpon*. A new non-native *Amaranthus* – *A. viridis* L. was recognized in California recently (Daniel 2005). Besides *Hedera helix* L. and *H. canariensis* Willd., plants derived from *H. hibernica* (Kircher) Bean seem to be quite common (Clarke et al. 2006). The correct name for spotted knapweed seems to be *Centaurea stoebe* L. subsp. *micranthos* (S.G. Gmelin ex Gugler) Hayek. Authors' note that Californian spotted knapweeds may be primarily classified as C. vallesiaca (DC.) Jord., species known from France, Italy and Switzerland, would deserve some elaboration. The fact that most of the *Raphanus* plants in California are hybrids (Panetsos and Baker 1967) is not mentioned. Good photos or drawings of lemma tips would help to make a distinction between *Avena barbata* and *A. fatua*. There are 31 species in the main text that were not included in *The Jepson Manual* (23 of them were recently reported by Hrusa et al. 2002). This is not always clearly indicated. Four species included in the main text are not present in California (*Brassica elongata*, *Hieracium caespitosum*, *Salsola collina*, and *Vinca minor*). This can be justified because some of them could be found in California in the foreseeable future. Including more pictures of species that are common and difficult in other mediterranean areas and are still rare or absent in California would make a weed manual even more helpful in early detection of potentially pestiferous invaders. Examples include *Atriplex numularia* Lindl., *Galega officinalis* L., *Leptospermum laevigatum* (Gaertn.) F. Muell., *Melia azedarach* L., *Paraserianthes* (*Albizia*) *lophantha* (Willd.) Nielsen, *Rosa moschata* J. Herrm (Henderson 2001; Mathei 1995). While the number of native weeds was definitely somewhat inflated in Robbins et al. (1951), several important native weeds are missing here. This is particularly true for weeds in forest plantations (see e.g., Tab. 2–3 in Walstad and Kuch 1987).

There are 722 non-native taxa listed in the Appendix. After excluding subspecific taxa and two species that were already treated in the main text, we are left with 714 alien species. Two of them are here by a mistake and should be deleted (*Acer saccharum* and *Genista aetnensis*). Most of the species (435) were already in *The Jepson Manual* (Hickman 1993). Among remaining 277 species (most of them are marked by asterisk), 261 were presented in Hrusa et al. (2002). Unfortunately, this was not acknowledged and neither was the origin of the information for the remaining 16 species. Nevertheless, one would expect that adding 673 non-native species from the main text to 712 non-native species from the

Appendix, the total of 1385 should equal the number naturalized and casual plant species in California. However, there are three problems here. First, some non-native species that were included in DiTomaso and Healy's (2003) previous book on wetland weeds appeared in the main text or in the Appendix, but some did not (e.g., *Aeschynomene rudis*, *Heteranthera limosa*, *Limnobium laevigatum*, *Najas graminea*, *Potamogeton crispus*, *Rotala indica*). Second, some established non-native species that are in *The Jepson Manual* are not in this Appendix (e.g., *Cnicus benedictus*, *Chenopodium strictum*, *Lathyrus sphaericus*, *Mollugo cerviana*, *Plantago virginica*, *Rumex orbiculatus*). Third, several species that were reported in Hrusa et al. (2002) are also missing in the Appendix (including *Asclepias fruticosa*, *Chrysanthemum balsamita*, *Silene pseudatocion*, *Ipomea quamoclit*, *Ephedra distachya*, *Cinnamonum camphora*, *Papaver capreolata*, *Passiflora mixta*). Therefore, we may conclude that we have ca. 1400 more or less established non-native plant species in California. Nobody will ever get the definite number. Some species probably do not grow in California any more (e.g., *Agrostema githago*) and some were probably eradicated (e.g., *Carthamus leucocaulos*, *Cuscuta reflexa*, *Grindelia papposa*, *Peganum harmala*, *Salvia virgata*, *Solanum cardiophyllum*, *Tagetes minuta*). Some species should not be counted because they are only persisting (e.g., *Jugnans regia*) or grow only in greenhouses (e.g., *Muntingia calabura*). On the other hand, new species are arriving (Jepson Flora Project 2007), and some "native" species – *Phalaris arundinacea*, *Spirodela* (*Landoltia*) *punctata* - are being recognized as exotics (Jacono 2002; Lavergne and Molofsky 2007).

The weakest part of this manual is the Bibliography (pp. 1680–1740). It is only slightly better than the one that was in DiTomaso and Healy's (2003) previous book that I reviewed for Madroño in 2003. First, General References: There are several obscure references here, but relevant basic publications on Californian weeds or invasive plants in general are missing (e.g., Baker 1962, 1974, 1986, 1995; Inerjit 2005; Myers and Bazely 2003; Pyšek et al. 2004; Randall et al. 1998; Rejmánek and Pitcairn 2002; Walstad and Kuch 1987; Weber 2003). Second, as for individual genera, references are far from balanced: e.g., 12 references to *Kyllinga* and 29 to *Taeniatherum*, but none to *Amsinckia*, *Bidens*, *Foeniculum*, *Hypericum*, *Raphanus*, *Viscum*, *Xanthium*, etc. References to *Anthemis cotula* are under *Cotula*. Gerlach's excellent studies of *Centaurea solstitialis* in California are missing (Gerlach and Rice 2003; Gerlach 2004). Ten, mostly Australian, references are under *Chondrilla*, but the most important reference to its biocontrol in California (Supkoff et al. 1988) is not listed. Again, many bizarre references (e.g., "Wild Flowers of Mount Olympus") are here, but essential references to such Californian weeds like *Carpobrotus chilensis*, *Mesembryanthemum crystallinum*, *Prosopis*, *Salsola*, or *Toxicodendron diversilobum* (Bicknell and Mackey 1998; Vivrette and Muller 1977; Holland 1987; Gaskina et al. 2006; Ryan and Ayers 2000; Gartner 1991a, b) are missing. A reference to the bibliography of European biological floras (Poschod et al. 1996) would be helpful.

Obviously, while the main body of this treatment is undoubtedly a great achievement, the value of the Appendix and Bibliography is rather questionable. My recommendation for the potential next edition of this manual would be to make it more economical (e.g., some redundant photographs could be deleted, pictures of seeds for all species in each genus could be combined into one), delete the Appendix and Bibliography (more professional version could be available online), and publish everything in one user-friendly volume. Recently published Flora of the Santa Ana River (Clarke et al. 2007) can serve as an example of how this could be done.

In spite of my criticism, this is a monumental piece of work. Even with digital cameras you have to find the plants first. The authors found almost all of them!

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American Perceptions of Immigrant and Invasive Species: Strangers on the Land. By Peter Coates. 2007. University of California Press, Berkeley, CA. 266 pp. Hardcover. $39.95. ISBN 13: 978-0-520-24930-1.

One of the defining characteristics of humans is their tendency to want to manage nature so that it meets their perceptions of "how things should be." Ecologically, this has been translated in numerous ways, from wildlife management practices that once promoted intense predator control to notions of restoring landscapes to "pre-European conditions." Of course, these perceptions are not universally accepted at any given point in time, and perhaps more important the prevailing opinion (i.e., conventional wisdom) often shifts over time. Hence, we now see the reintroduction of predators into areas they were once extirpated from, and the gradual realization by restoration practitioners that trying to convert an ecosystem to an arbitrary point in time (and then keeping it there) is fraught with both conceptual and practical problems. In *American Perceptions of Immigrant and Invasive Species*, Peter Coates, an environmental historian at the University of Bristol, uses historical and contemporary case studies to analyze views on non-native species in the United States over the last

two centuries. But rather than limiting his analysis to an ecological viewpoint, Coates poses the question of whether our attitudes towards non-native plants and animals have simply been a reflection of the prevailing way American society thinks about immigrants in general, or whether the two issues are essentially independent of one another. By doing this, he places the issue of biological invasions in a broader context of social and cultural perceptions than they are typically found. One of the tangible achievements of Coates book is that it clearly shows that perceptions of "how things should be" depends on where and when you are standing in a certain place, a lesson that scientists and conservation practitioners too frequently forget.

In many ways, *American Perceptions of Immigrant and Invasive Species* is an extension of Coates' earlier book *Nature: Western Attitudes Since Ancient Times*, (Blackwell Publishers 1998). Coates employs the same approach here as he did in *Nature*. Using history as his pathway, he describes the development of perceptions towards natural phenomena both within and across given periods of times, with the path ultimately ending in our own contemporary era. Though he does not ignore their philosophical underpinnings, Coates is an empiricist at heart and is more interested in the cultural manifestations and social outcomes of our perceptions than their logic or intellectual merit. Indeed, Coates uses their contradictions to illuminate from where these perceptions arise and how they become part of our collective psyche. In the case of *American Perceptions of Immigrant and Invasive Species*, he has simply narrowed his scope from broad views of nature to specific views on a particular, albeit highly charged, part of nature.

Coates structures the five-chaptered book in two ways. One is used to develop the general themes that cut across the individual chapters and unite the case studies. The other is the approach he uses within the individual chapters. Coates presents an initial overview of the specific topic in the opening section of each chapter, including its issues, time period, and major players. He then uses the remainder of the chapter to dive into the details. This allows Coates to deepen each case study with scholarly particulars, but by maintaining a coherent thread that runs throughout the book the general themes are never lost in minutiae.

In the introductory chapter, Coates explains the importance of what is in a name, depicts the tendency of humans to transfer human qualities to species and species qualities to humans, and makes initial comparisons between opinions towards biological invasions and human immigration. Perhaps most important, he sets the stage for the stark contrast between the opinions of those who adhere to the philosophy that native born species, or individual humans, are best suited for an area (the "nativist" philosophy) and those who feel that local qualities are vastly improved with infusions from other areas (the "cosmopolitanist" philosophy). In one way or another, it is the conflict between the nativists and the cosmopolitanists that plays out across the next four chapters. Chapters 2–4 are largely on historical events. They describe the contributing factors and often heated debates surrounding the introduction and spread of the house sparrow, (and to a lesser degree the starling; Chapter 2), agricultural crops and their pests and pathogens (Chapter 3), and tree-of-heaven and eucalyptus (Chapter 4). In Chapter 5, Coates returns to his broader themes by focusing on the controversies surrounding human immigrants and biological invasions in our era. My guess is most readers of the book will find Chapter 5, as well as the latter part of Chapter 4, the most accessible because the case studies are largely contemporary. However, it is in Chapter 3 where the debate between the nativist and the cosmopolitanist schools best informs us of where our deeper perceptions, and inherently contradictory attitudes, towards non-native species can lead us.

Coates is a good enough writer and thorough enough thinker that, overall, the book is a lively and absorbing read. Having said that, it is important to point out that while it is not technical by any stretch of the imagination, the book is nevertheless an academic publication that is dense in detail. Most of the time the detail adds color and depth to the narrative, but in some places it can make it difficult to follow, especially when trying to link some of the more obscure players to specific events or ideas attributed to them several pages (or even chapters) back. Though this makes the book less accessible as popular reading, the tradeoff is that it is an intelligent and scholarly work that never wanders into the often sensationalist and shallow writing not uncommonly found in non-technical pieces on both non-native species and immigration. Although Coates has his opinions, they tend to illuminate rather than consciously skew the issues. His insights and subject matter remain vibrant, and he is adept at drawing the details together into a coherent whole at the end of each chapter.

The book does have one flaw. Coates seems to have tried to make a compromise between the depth and breadth of the book (something that also characterized *Nature*). He did a very admirable job mining the depths of his three case studies; of the books 256 pages, 189 are devoted to narrative and the rest to footnotes. But what was gained in detail resulted in a sacrifice in breadth. Drawing general conclusions from the three main case studies is difficult because they are not entirely representative of the way other

species introductions in North America have played out. The book would have had greater breadth had Coates included one or two additional case studies that broadened the debate. He undoubtedly picked his case studies strategically because they provided the links he was seeking between invasive species and immigration, especially for examining these links across time periods and shifting social and cultural values. In some ways though, the stories of house sparrows and starlings and eucalyptus and many agricultural crops are old news. They have been well-documented, and the stories all play out more or less in the same way. Overlooked or only given scant mention are stories of other introduced non-native species that have been less contentious, or, up until modern times, considered to be of benefit to humans. This includes game animals such as ring-necked pheasants, chukar, brown trout, and wild boar, and trees such as the European olive and fig. The question of when a species ceases to become native and becomes an invasive and harmful non-native is a critical one and is almost entirely ignored. Mountain goats in Olympic National Park, horses in parts of the arid and semi-arid western United States, some fish species (e.g., rainbow and brook trout), and plants such as yellow bush lupine are either native to some regions of the country, a state, or a bioregion, but not others, or they were native to the continent in relatively recent times. These are provocative examples of the capricious way humans continue to decide what belongs in an ecosystem and what does not, and could have provided broader insights into our perceptions of non-native species introductions. As compelling a book as *American Perceptions of Immigrant and Invasive Species* is, it probably would have been even more so if Coates had picked some of these lesser known but equally telling examples as case studies.

Nevertheless, while the stories of house sparrows and starlings and eucalyptus have been fodder for discussion for decades, many people involved in research and management of invasive non-native species have forgotten that their concerns are not new ones. It is even debatable whether the topic is any more heated or complex now than it was a century ago. The singular strength of this book is that it highlights that, in many ways, the issues and controversies that surround species introductions have been ongoing for centuries, and in many ways they have not changed substantially. They have only been translated into the value sets, language, and perceptions unique to our time. For this reason alone, the book is a highly informative work that provides useful insights not just for people doing work on non-native species, but ecologists and conservationists in general.

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NOTEWORTHY COLLECTIONS

BRITISH COLUMBIA

SPIRANTHES DILUVIALIS SHEVIAK (ORCHIDACEAE).—Southern Okanagan Valley, alkaline marsh, east shore of Osoyoos Lake, Oliver Indian Band Reserve, elev. 300 m, 11 August, 2006, *Björk 13671* (photo voucher housed at UBC), verified by Charles Sheviak; Southern Okanagan Valley, alkaline marsh, Mahoney Lake 49° 17′N, 119°34′W, elev. 550 m, 12 August, 2006, *Björk 13672* (photo voucher deposited at UBC).

Previous knowledge. A rare species of the central and western United States, where it is listed as Threatened by the U.S. Fish and Wildlife Service (Fertig, W., R. Black & P. Wolken. 2005. Rangewide Status Review of Ute Ladies'-Tresses (*Spiranthes diluvialis*). http://www.fws.gov/mountain-prairie/species/plants/uteladiestress/SPDI_Status%20review_Fertig2005.pdf Accessed 10 October, 2007.). Most populations are concentrated in the Rocky Mountains as far north as eastern Idaho and southwest Montana, but three outlier populations were recently discovered in Washington State, one of which is in the Okanogan Valley just south of the Canadian border.

Significance. First record for British Columbia and Canada, and a range extension of about 20 km northeast of the northernmost Washington population. Only a single plant was found at the Osoyoos Lake site, and six plants at Mahoney Lake. Several other regionally rare species are present at the Osoyoos Lake site, including some that are found nowhere else in Canada.

ELEOCHARIS GENICULATA (L.) ROEMER & SCHULTES (CYPERACEAE).—Southern Okanagan Valley, mud flats near east shore of Osoyoos Lake, Oliver Indian Band Reserve, elev. 300 m, 12 August, 2006, *Björk 13673* (UBC).

Previous knowledge. A widespread species of tropical and warm temperate regions. In America north of Mexico, *E. geniculata* is known from a scattered range across the southern and eastern portions of the United States, north to Ontario (Menapace, F.J. 2002. Eleocharis R. Brown (subg. Eleocharis sect. Eleogenus) ser. Maculosae *in* Flora of North America Editorial Committee. Flora of North America. Vol. 23. New York. Oxford University Press. 640 pp.).

Significance. First record for British Columbia. Our record of this plant comes from the same site as historic reports of *Eleocharis atropurpurea*. The close similarity of that species to *E. geniculata* and our inability to find *E. atropurpurea* in two summers of searching in the landscape from which it was historically reported led us to believe that *E. atropurpurea* was misapplied to this population of *E. geniculata*. Examination of the historical collections (1939, 1991) and of our 2005 and 2006 collections and comparison with specimens of both species from the Jepson Herbarium support that the species that has been previously collected at Osoyoos and is still extant there is *E. geniculata*. Since Osoyoos Lake was the only known location in British Columbia and Canada for '*E. atropurpurea*', we believe that species should be removed from lists of plant species native to the province and the country and replaced by *E. geniculata*. Despite the often weedy habit of *E. geniculata*, we believe that it is native at the site since it grows there with a large number of other wetland plants characteristic of warm-temperate climates, and since collections previously thought to be *E. atropurpurea* were made very early at Osoyoos Lake (1939), before the advent of most nonnative plant invasions in southern British Columbia.

LIMOSELLA ACAULIS SESSÉ & MOCIÑO (PLANTAGINACEAE).—Southern Okanagan Valley, mud flats near east shore of Osoyoos Lake, Oliver Indian Band Reserve, elev. 300 m, 12 August, 2006, *Björk 13674* (UBC).

Previous knowledge. Western United States and Mexico (Wetherwax, M. 1993. Limosella *in* Hickman, J.C., ed. 1993. Jepson Manual: Higher Plants of California. Berkeley. University of California Press. 1424 pp.). It is uncommon in Washington in the northwestern United States, and was only recently first discovered for Idaho (Björk unpublished).

Significance. First record for British Columbia and Canada and a range extension of 250 km north from the nearest populations in Washington.

CRYPSIS ALOPECUROIDES (PILLER & MITTERP.) SCHRAD. (POACEAE).—Southern Okanagan Valley, mud flats near east shore of Osoyoos Lake, Oliver Indian Band Reserve, elev. 300 m, date 12 August, 2006, *Björk 13675* (UBC).

Previous knowledge. Native to warm-temperate Eurasia, south to northern Africa and Iraq (Hammel, B.E. & J.R. Reeder. 2003. Crypsis *in* Flora of North America Editorial Committee. Flora of North America. Vol. 25. New York. Oxford University Press. 783 pp.). A widespread introduction in the western United States, previously known as far north as Spokane County, Washington (Björk unpublished).

Significance. First record for British Columbia and Canada for this species and genus. It forms dense populations in mud flats that are of high conservation priority due to the large number of nationally rare species.

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CIRSIUM FLODMANII (RYDB.) ARTHUR (ASTERACEAE).—Southern Okanagan Valley, sagebrush steppe WNW of White Lake, lat/longs 49°18′N, 119°39′W, elev. ~600 m, 11 August, 2006, *Björk 13990* (UBC).

Previous knowledge. Central North America from the Canadian Prairie Provinces south to Colorado and Minnesota (Keil, D.J. 2006. Cirsium *in* Flora of North America Editorial Committee. Flora of North America. Vol. 19. New York. Oxford University Press. 610 pp.), with an outlier population in the Okanogan Valley of Washington (Björk unpublished).

Significance. First record for British Columbia and a range extension of 120 km north from the single Washington population. Possibly previously over-

looked probably due to the species' close resemblance to the common and widespread *C. undulatum*. Apparently native and one of a significant number of Great Plains and Rocky Mountains species that are disjunct in the Okanagan.

VIOLA ADUNCA SM. VAR. *CASCADENSIS* (BAKER) C.L. HITCHCOCK (VIOLACEAE).—Southern Okanagan Valley, interface of ponderosa pine forest and salt-flat vegetation at the north end of Mahoney Lake, 49°17′N, 119°35′W, elev. 550 m, 11 August, 2006, *Björk 13991* (UBC).

Previous knowledge. East slopes of the Cascades and the Okanogan Valley, in Washington and Oregon (Hitchcock, C.L., & A. Cronquist. 1973. Flora of the Pacific Northwest: an Illustrated Manual. Seattle. University of Washington Press. 730 pp.).

Significance. First record for British Columbia and Canada and a range extension of about 20 km. This is a distinct variety, but is seldom recorded as the variety, so its rarity is difficult to assess.

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ANTENNARIA CORYMBOSA E. NELS. (ASTERACEAE).—Cariboo Mountains, margin of *Carex utriculata* fen, headwaters of the Blue River, 52°04′N, 119°33′W, 1000 m elev., 24 July, 2004, *Björk 9415* (UBC).

Previous knowledge. Western United States, mostly in the Rocky Mountains (Bayer, R.J. 2006. Antennaria *in* Flora of North America Editorial Committee. Flora of North America. Vol. 19. New York. Oxford University Press. 610 pp.).

Significance. First verified record for British Columbia and Canada and a range extension of about 450 km from the nearest population in northeast Washington. This is an ecologically distinctive species, being one of few in the genus that can tolerate the wet, peaty soil of marshes and fens.

FESTUCA WASHINGTONICA E.B. ALEXEEV (POACEAE).—Southern Okanagan Valley, Grassland-woodland mosaic, Richter Pass, southeast slopes of Mount Kobau, 49° 06′N 119° 37′W, 1200 m elev., verified by Stephen Darbyshire.

Previous knowledge. East slopes and foothills of the Cascade Mountains in Washington State (Darbyshire, S. 2007. Festuca *in* Flora of North America Editorial Committee. Flora of North America. Vol. 24. New York. Oxford University Press. 944 pp.), known from few populations scattered between Rattlesnake Mountain in Franklin County, north to near Loomis in Okanogan County (Björk unpublished).

Significance. First valid record for British Columbia and Canada, and a range extension of about 30 km north of the northernmost Washington population. Very few individuals were present, but the species tends to grow at elevations higher than 1200 m, so the collection site might represent the lower edge of a larger population. In Volume 24 of the Flora of North America, the presently cited specimen was the basis for a British Columbia dot on the distribution map, but the dot appears on Vancouver Island, where this species would not likely find suitable habitat.

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CALIFORNIA

ALLOPHYLLUM DIVARICATUM (NUTT.) A. D. Grant & V. Grant (POLEMONIACEAE).—Riverside Co., Peninsular Ranges Province, San Jacinto Mountains region, upper Tahquitz Valley, elev. 2408 m (7900 ft.), 19 Jul 1933, *Dunkle 3675* [det. A. Day, 1980] (RSA); San Jacinto Mountains, burned slope in chaparral on Banning- Idyllwild Rd., elev. 914 m (3000 ft), *McKinley 680305-4*, 4 May 1968 (UCR); trail to Spitler Peak from Hurkey Creek Campground, Bonita Vista Rd., T5S R3E N1/2 Sec. 35, elev. 1707 m (5600 ft), growing in chaparral and yellow pine forest, 1 Jun 1986, *Sanders 6548* (UCR); N side along Hwy 243, 1.5 mi. below Twin Pines Ranch Road (McMullen Flat), N slope of peak, 33°53.1′N, 116°51.5′W, T3S R1E SW/4 S23, elev. 1067 m (3500 ft), 4 May 1997, *Sanders et al. 20633* (UCR, RSA); along Hwy 243, 1–2 mi. below Mt. Edna turnoff, 14 May 1988, *Harper s.n.* (RSA); near Mountain Center, unnamed ephemeral drainage, tributary to S Fork, San Jacinto River, Idyllwild, 33° 41.5′N, 116°44′W, T5S R2E S36, SW, elev. 1402–1463 m (4600–4800 ft), 5 Aug 2000, *White 8113* (RSA); Peninsular Ranges Province, Agua Tibia Mountains region, SE of Temecula, Cleveland National Forest, Agua Tibia Wilderness, NW slope of Agua Tibia Mountain, ca. 1.5 mi WNW of Woodchuck Rd., USGS 7.5' Pechanga Quadrangle, UTM (NAD 83) 11S 0497415E 3699899N, elev. 665 m (2180 ft), locally common to widely scattered in open oak riparian forests and on sandy benches along unnamed blueline stream, 31 Jul 2005, *Riefner 05-573* [annotated J. M. Porter, 2005] (RSA). San Diego Co., Peninsular Ranges Province: W slope of Agua Tibia Mountains, headwaters of Pala Creek, USGS 7.5' Pechanga Quadrangle, UTM (NAD 83) 11S 0494408E 3698202N, elev. 488 m (1600 ft), widely scattered on sandy benches in mesic chaparral, 3 Jul 2005, *Riefner 05-542* [annotated J. M. Porter, 2005] (RSA).

Previous knowledge. Allophyllum divaricatum (purple false-gilia) occupies sandy areas in chaparral and woodlands from 300–1800 m in the Klamath Ranges, Inner North Coast Ranges, South Cascade Ranges, Sierra Nevada Foothills, San Francisco Bay Region, South Coast Ranges, and the Transverse Ranges (Day 1993, *in* Hickman, ed., The Jepson Manual: Higher Plants of California, University of California Press, Berkeley, CA).

Significance. First reports of *A. divaricatum* documented from the Peninsular Ranges Province (Day 1993 *loc. cit.*). In addition, the collections from the Agua Tibia Mountains represent the first documented records for western Riverside County and San Diego County (Banks 1999, A Vascular Flora of the Agua Tibia Mountains, Southern California, Rancho Santa Ana Botanical Garden Occasional Publications No. 4, Claremont, CA; Roberts et al. 2004, The Vascular Plants of Western Riverside County, California: An Annotated Checklist, F. M. Roberts Publications, San Luis Rey, CA; Rebman and Simpson 2006, Checklist of the Vascular Plants of San Diego County, ed. 4, San Diego Natural History Museum, San Diego). The occurrence of *A. divaricatum* in low-elevation canyons

and on valley slopes in the Agua Tibia Mountains may be attributed to cold-air drainage patterns that produce localized fog, which is significant to vegetation because it reduces water lost by transpiration (Schoenherr 1992, A Natural History of California, California Natural History Guide No. 56, University of California Press, Berkeley, CA). Cold-air drainage is a phenomenon that results from the diurnal effect of dense cold air that forms on the tops of mountains or ridgelines that drains into and replaces less dense warm air in canyons or over valley floors of surrounding lowlands (Bailey 1996, The Climate of Southern California, California Natural History Guide No. 17, University of California Press, Berkeley). Throughout the Agua Tibia Mountains, cold-air drainage is also likely responsible for the distribution and occurrence of *Abies concolor* (Gordon & Glend.) Lindley, *Artemisia tridentata* Nutt., *Calocedrus decurrens* (Torr.) Florin, *Monardella macrantha* A. Gray subsp. *hallii* Abrams, *Pseudotsuga macrocarpa* (Vasey) Meyer, and *Sedum spathulatum* Hook. in canyons and valleys at elevations hundreds of meters lower than usual (Banks 1999 *loc. cit.*).

CARDIONEMA RAMOSISSIMUM (J. A. Weinmann) A. Nelson & J. F. Macbride (CARYOPHYLLACEAE).—Riverside Co., Temecula Valley, Rainbow Canyon Rd. ca. 0.7 mi N of Pechanga Pkwy., S of the Temecula Creek Golf Course, USGS 7.5' Temecula Quadrangle, UTM (NAD 83) 11S 0488229E 3702224N, elev. 340 m (1115 ft), widely scattered in sandy coastal sage scrub and along dirt roads, 30 May 2006, *Riefner 06-216* (RSA).

Previous knowledge. *Cardionema ramosissimum* (sand mat or tread lightly) occupies sandy beaches and hills, dunes, and grassy bluffs below 200 m elevation in the North Coast Ranges, Central Coast, and South Coast regions of California, and along the Pacific coasts of Oregon, Washington, Mexico, and disjunct to the Pacific coasts of Chile, Ecuador, and Peru in South America (Hartman 1993, *in* Hickman, ed., The Jepson Manual: Higher Plants of California, University of California Press, Berkeley; Hartman 2005, *in* Flora of North America Editorial Committee, eds., Flora of North America, Vol. 5, Magnoliophyta: Caryophyllidae, Part 2, Oxford University Press, New York). In southwestern California, *C. ramosissimum* is well known from the coastal plains and foothills of Los Angeles, Orange, and San Diego counties, but not from the inland valleys of western Riverside County (Roberts et al. 2004 *loc. cit.*).

Significance. First record documented for Riverside County (Hartman 1993 *loc. cit.*; Hartman 2005 *loc. cit.* Roberts et al. 2004 *loc. cit.*). In southern California, *C. ramosissimum* is rare or absent away from the immediate coast, with the exception of the interior valleys influenced by maritime breezes, such as near Pala in the San Luis Rey River valley, San Diego County (Banks 1999 *loc. cit.*). Inland penetration of the marine layer, a dense layer of clouds, reduces evapotranspiration rates and lowers temperatures, which contributes significantly to soil moisture through fog-drip precipitation (Schoenherr 1992 *loc. cit.*). In the Temecula Valley and on the western slopes of the Agua Tibia Mountains in western Riverside County, the cooling effect of the marine layer is a local weather phenomenon important in determining species distribution and plant community composition (Banks 1999 *loc. cit.*). Other typically coastal species that are locally common or known to occur historically only in the Temecula Valley or other areas of western Riverside County influenced by maritime breezes, includes *Baccharis pilularis* DC., *Cylindropuntia prolifera* (Engelm.) F.M. Kunth, and *Malosma laurina* (Nutt.) Nutt ex Abrams (Roberts et al. 2004 *loc. cit.*).

CEANOTHUS IMPRESSUS Trel. var. *IMPRESSUS* (RHAMNACEAE).—Los Angeles Co., E of Sunland, Verdugo Mountains, N side of 210 Freeway, W ca. 0.6 mi from the intersection of La Tuna Canyon Rd. with the 210-Freeway, USGS 7.5' Burbank Quadrangle, UTM (NAD 83) 11S 0380138E 3789150N, 475 m (1558 ft), single shrub on old fill slope, 12 Jun 2006, *Riefner 06-238* (RSA).

Previous knowledge. *Ceanothus impressus* var. *impressus* (Santa Barbara wild lilac) grows on dry sandy mesas, coastal terraces, and bluffs in chaparral, and open oak woodlands below 200 m elevation in the Central Coast Region (Schmidt 1993, *in* Hickman, ed., The Jepson Manual: Higher Plants of California, University of California Press, Berkeley; Fross and Wilken 2006, Ceanothus, Timber Press, Portland, Oregon). The var. *impressus* appears to be restricted to the bluffs and terraces of Burton Mesa in western Santa Barbara County, and is a species of local concern (Fross and Wilken 2006 *loc. cit.*).

Significance. First record *C. impressus* var. *impressus* documented for Los Angeles County (Schmidt 1993 *loc. cit.*; Fross and Wilken 2006 *loc. cit.*). Likely introduced in a hydroseed mix, its occurrence on a freeway fill slope in the Verdugo Mountains demonstrates the need to develop statewide planting guidelines to prevent artificial extensions of range of sensitive plant taxa.

LYCIUM BREVIPES Benth. var. *BREVIPES* (SOLANACEAE).—Orange Co., City of San Clemente, vicinity of San Clemente Pier and Ave. Del Mar, USGS 7.5' Linda Lane Park, San Clemente Quadrangle, UTM (NAD 83) 11S 0442054E 3698390N, 3 m (10 ft), locally common in coastal bluff scrub, 23 Dec 2004, *Riefner 04-558* (RSA); City of Corona del Mar, vicinity of Poppy Ave. and Ocean Blvd., USGS 7.5' Buck Gully, Laguna Beach Quadrangle, UTM (NAD 83) 11S 0419429E 3716996N, 4 m (13 ft), locally common in coastal bluff scrub, 6 Sep 2006, *Riefner 06-419* (RSA).

Previous knowledge. *Lycium brevipes* var. *brevipes* (common desert thorn) grows on coastal bluffs and slopes below 600 m elevation in the South Coast Region, the Channel Islands, the western Sonoran Desert, and in Mexico (Nee 1993 *in* Hickman, ed., The Jepson Manual: Higher Plants of California, University of California Press, Berkeley). A collection of *Lycium brevipes* var. *brevipes* from Orange County, City of San Clemente, south of the intersection of Ave. Calafia and Ola Vista St. (*Reiser s.n.*, 21 Mar 2001, SD), is referable to the population previously determined to be *Lycium brevipes* var. *hassei* (Greene) C. L. Hitchc. (*Riefner 95-77*, 12 Mar 1995, RSA). The *Riefner 95-77* material compared favorably with the type specimen of *L. hassei* Greene collected from Catalina Island (*Hasse & Lyon s.n.*, NDG !). The var. *hassei* is separated from the typical variety by the spatulate to narrowly obovate calyx lobes, 1 to 3 times as long as the tube versus the linear to triangular calyx lobes, 1/3 as long or equal to the tube for the var. *brevipes* (Nee 1993 *loc. cit.*). However, this subtle distinction in the size and shape of the calyx lobes may not be readily apparent during early flowering stages of the shrub. Ongoing observations

and collections of taxa in the *L. brevipes* complex that overlap in northern San Diego and southern Orange counties indicate the spatulate calyx lobes of the var. *hassei* become foliose in fruit, and the linear to triangular calyx lobes of the var. *brevipes* do not (Riefner and Boyd unpublished data). However, based on overlapping ranges and habitats, similarity in habit and phenology, additional study is needed to resolve the uncertain taxonomic distinctiveness of *L. brevipes* var. *hassei*, which has been raised previously by Skinner et al. (1995, Madroño 42: 211–241).

Significance. First documented records for the var. *brevipes* in Orange County (Roberts 1998, A Checklist of the Vascular Plants of Orange County, California, ed. 2, F.M. Roberts Publications, Encinitas, CA). These collections likely represent the northwestern-most known limit of its range in the South Coast Region.

PARIETARIA JUDAICA L. (URTICACEAE).—Los Angeles Co., City of San Pedro, Point Fermin, USGS 7.5' San Pedro Quadrangle, UTM (NAD 83) 11S 0380915E 3730581N, elev. 13 m (41 ft), common on disturbed coastal bluffs and coastal strand habitats with *Atriplex semibaccata*, *Beta vulgaris*, *Distichlis spicata*, *Rhus integrifolia*, and *Rumex crispus*, 12 Jan 2006, *Riefner 06-13* (RSA, UCR); City of San Pedro, San Pedro Bay, Adams Drive St. at Miner St., USGS 7.5' San Pedro Quadrangle, UTM (NAD 83) 11S 0380915E 3730581N, elev. 3 m (9 ft), common on rocky bay shores with *Atriplex triangularis* and *Suaeda taxifolia*, 29 Jul 2006, *Riefner 06-331* (RSA, UCR). Orange County, City of Huntington Beach, Beach Blvd. at MacDonald St., USGS 7.5' Newport Beach Quadrangle, UTM (NAD 83) 11S 0408290E 3732120N, elev. 6 m (18 ft), common in urban irrigated landscape, 21 May 2006, *Riefner 06-199* (RSA); City of Huntington Beach, Huntington Central Park at Goldenwest St., USGS 7.5' Seal Beach Quadrangle, UTM (NAD 83) 11S 0406841E 3729999N, elev. 4 m (14 ft), uncommon, growing in disturbed *Salix*-dominated riparian woodland, 28 Jul 2006, *Riefner 06-325* (RSA).

Previous knowledge. Parietaria judaica (spreading pellitory), native to Eurasia and North Africa, grows in cracks in sidewalks, ballast heaps, waste places, and about ports in coastal areas of California, Florida, Louisiana, Michigan, New Jersey, New York, Pennsylvania, and Texas (Boufford 1997, *in* Flora of North America Editorial Committee, eds., Flora of North America, Vol. 3, Magnoliophyta: Magnoliidae and Hamamelidae, Oxford University Press, New York). In North America, it is most abundant at scattered localities in California, where it is often invasive in coastal urban settings (Woodland 1993, *in* Hickman, ed., The Jepson Manual: Higher Plants of California, University of California Press, Berkeley, CA; Boufford 1997 *loc. cit.*).

Significance. First record of *P. judaica* documented for Orange County (Roberts 1998 *loc. cit.*); verification of records for Los Angeles County. *Parietaria judaica* is apparently spreading from urban environments to mesic, native plant habitats in the south coast region. It is expected elsewhere, including other native habitats and urban settings in Los Angeles, Orange, Riverside, San Diego, and Ventura counties.

RHAMNUS PILOSA (TREL.) Abrams (RHAMNACEAE).—Riverside Co., E of Rainbow Canyon, N of Rainbow Heights, Termite's Hike Trail, USGS 7.5' Pechanga Quadrangle, UTM (NAD 83) 11S 0490089E 3699743N, elev. 614 m (2013 ft), widely scattered in rocky, mesic chaparral, 11 Oct 2006, *Riefner 06-529* (RSA).

Previous knowledge. Rhamnus pilosa (hairy-leaf redberry) is an uncommon shrub that grows in chaparral from 300–700 m elevation in the Peninsular Ranges and in Baja California, Mexico (Sawyer 1993, *in* Hickman, ed., The Jepson Manual: Higher Plants of California, University of California Press, Berkeley). It has been collected from San Diego County, but not from Orange or western Riverside counties (Roberts 1998 *loc. cit.*; Roberts et al. 2004 *loc. cit.*; Rebman and Simpson 2006 *loc. cit.*).

Significance. First record documented for Riverside County (Roberts et al. 2004 *loc. cit.*). *Rhamnus pilosa* is widespread in the general Rainbow Canyon area, but is most abundant in mesic chaparral developed on gabbro substrates. It is often closely associated with a number of plants that are uncommon in western Riverside County, including *Arctostaphylos rainbowensis* Keeley & Massihi, *Calamagrostis densa* Vasey, *Hesperolinon micranthum* A. Gray, *Salvia clevelandii* (A. Gray) Greene, *Senecio ganderi* T. Barkley & Beauch., and *Tetracoccus dioicus* C. Parry (Banks 1999 *loc. cit.*; California Native Plant Society 2001, Inventory of Rare and Endangered Vascular Plants of California, ed. 6, Rare Plant Scientific Advisory Committee, D. Tibor, ed., California Native Plant Society, Sacramento, CA; Roberts et al. 2004 *loc. cit.*).

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CALIFORNIA

BOERHAVIA DIFFUSA L. (NYCTAGINACEAE).—Yolo Co., West Sacramento, off West Capitol Avenue, ~0.5 mi. E of eastern levee of Yolo Bypass. Disturbed sandy soil, with *Salsola* sp. and *Polygonum* cf. *aviculare*. Flat mat on ground, 0.5 m across,1 plant, near drainage ditch heading N from West Capitol Avenue. A. M. Shapiro *s.n.*, August 26, 2005 (DAV). Near 38°34′40.2″N, 121°34′08.5″W, 2 m elev. Determination confirmed by Richard Spellenberg May 12, 2006.

Previous knowledge. Boerhavia diffusa (common name: spreading hogweed or red spiderling) is found worldwide in the tropics and subtropics and is occasionally known from riparian areas in drier regions of the world. In the United States, *B. diffusa* is currently found in Florida, Georgia, South Carolina, and North Carolina, and there are reports from Alabama, Louisiana, and Texas. There has been no suggestion to date that this species is even likely to occur in California. *Boerhavia* is a taxonomically difficult genus with often subtle characters. Many *Boerhavia* taxa that are morphologically distinct in most of their range often tend to intergrade with related taxa when ranges overlap. *B. diffusa*, because of its morphological variability over its worldwide range, has been treated variously by past authors to include one or two species (R. Spellenberg, 2004, in *Flora of North America North of Mexico*, v. 4, Oxford University Press: 19–20).

Further taxonomic complication has arisen over the uncertain typification of *B. diffusa*. Fosberg (Fosberg, F. R., 1978, Smithsonian Contributions to Botany 39: 4–5.), in his examination of the typification of *B. diffusa*, noted that the differences between multiple named taxa in the New World (*B. paniculata* Richard, *B. coccinea* Mill., *B. caribaea* Jacq., *B. viscosa* Lag. & Rodr., and *B. hirsuta* Willd.) and *B. diffusa* had "not yet been worked out to [his] satisfaction, but several species probably exist in this complex." Fosberg, however, mistakenly lectotypified *B. diffusa* on a specimen that could not have been seen by Linnaeus until after the publication of *B. diffusa* in *Species Plantarum* (1753) and that disagreed with the protologue. This was later corrected by Whitehouse (Whitehouse, C., 1998, Taxon 47: 873–874) by conserving the name *Boerhavia diffusa* L. with a conserved type from the Virgin Islands (recommended for acceptance by the Committee for Spermatophyta in 2000, Taxon 49: 276–277). While there was a collection in the Linnean herbarium that was most likely the source of the original description of *B. diffusa* (No. 9.7, LINN), this material agrees with what is universally called *B. coccinea* today. For the sake of nomenclatural stability, Whitehouse typified *B. diffusa* on a specimen with terminal paniculate inflorescences to agree with accepted usage of the name. Taking this into account, Spellenberg correctly recognized both *B. diffusa* L. and *B. coccinea* Mill. for North America north of Mexico. Amongst the *Boerhavia* species known from California, *Boerhavia diffusa* most closely resembles and could easily be confused with *Boerhavia coccinea. Boerhavia diffusa* differs from *B. coccinea* by having glabrous stems and peduncles, leaves restricted to the lower half of the plant, terminal inflorescences, leaves glabrous excluding occasional minute puberulence and occasional multicellular hairs on veins, leaf veins prominent, flowers borne in clusters of 2–5, and fruits with a broadly conic apex formed by an abrupt bend in the fruit ribs near the fruit apex. Beauchamp (Beauchamp, M. R., 1986, *A Flora of San Diego County*, Sweetwater River Press) recognizes *B. coccinea* Mill. for the flora San Diego Co., and lists *B. diffusa* L. as a synonym. However, Linnaeus published *B. diffusa* some 15 yr before Miller published *B. coccinea*, thus *B. diffusa* has priority if one chooses to synonymize these two species. It is unclear how this species came to occur in central California, however *Boerhavia diffusa* is used medicinally and as a food plant in several parts of the world, and may have been introduced into California through cultivation.

Significance. This is the first record of this species in California. Since *Boerhavia diffusa* prefers a tropical environment, it is unlikely that this species will become a problematic invasive weed in most areas. However, in the tropics this species grows in dry, disturbed areas (including on exposed reefs), and could be to some degree preadapted for the California climate and modern disturbance regime. This plant has the potential to spread along riparian systems, and should be watched for in the future particularly along river corridors in California's Central Valley. Thanks to Art Shapiro for providing collection locality details, and to Rich Spellenberg for assistance with determination.

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ERRATUM

Soon after publication of the note on *Lathyrus* and *Vicia* (Broich 2007), it was pointed out that the selection of the epithet *sandbergii* T. White for the transfer of *Lathyrus bijugatus* T. White to the varietal level under *L. lanszwertii* Kellogg is incorrect. Under the current International Code of Botanical Nomenclature (Vienna Code, McNeill, et al. 2006), article 26.3 stipulates that when *L. bijugatus* T. White was published and the additional *L. bijugatus* var. *sandbergii* T. White was described, a variety *bijugatus* was established as an autonym. Under article 11.6 of the Code, the autonym has priority in the case of the transfer proposed by Broich (2007), since the two varieties are considered to be synonymous. Therefore, the correct nomenclatural proposal for this transfer is:

Lathyrus lanszwertii var. **bijugatus** (T. White) Broich comb. nov.

Lathyrus bijugatus T. White var. *bijugatus* T. White, Bull. Torrey Bot. Club 21:457, a priorable autonym. 1894. TYPE: Idaho: Latah Co., *J. H. Sandberg in 1892* (holotype NY!; isotype WS!). *Lathyrus bijugatus* var. *sandbergii* T. White. Bull. Torrey Bot. Club 21:457. 1894. TYPE: Idaho: Latah, Co., *J. H. Sandberg in 1892* (holotype NY!).

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PRESIDENT'S REPORT FOR VOLUME 54

I would like to welcome you to the 92nd year of the California Botanical Society. As we begin to approach the first century of our organization, I would like to thank all of the volunteers that are responsible for the continuing function of the Society. In particular, the board has been responsible and proactive in meeting all the challenges and duties involved in running a non-profit organization. So, I would like to extend my deep appreciation to Sue Bainbridge (Corresponding Secretary), Staci Markos (Recording Secretary), Stephania Mambelli (First Vice-President), Matt Ritter (Second Vice-President), Mike Vasey (Past President), Roy Buck (Treasurer), Abigail Moore (Student representative), Andrew Doran, Diane Ikeda, and Jim Shevock.

Speaking of *Madroño*, there are several major changes taking place. Hard-working editor John Hunter has completed his tenure. I would like to thank John for all of his efforts. Editing a peer-reviewed journal is a daunting task, and it takes a person with a strong sense of community responsibility to consent to do it. In that regard, I would like to welcome the new editor of *Madroño*, Paula Schiffman of California State University, Northridge. She will be following in the footsteps of many great California botanists, starting with W. L. Jepson.

In other personnel changes, Roy Buck, our long-time treasurer, will be stepping down from that role. Roy has provided an important consistency and organizational memory as he carried out the crucial tasks of treasurer, and I would like to extend to him special thanks. He will continue to serve on the board as a member-at-large. Stephania Mambelli has finished her term as Second Vice-President in charge of programming. Stephania's efficiency and effectiveness have made her a joy to work with. Member-at-large, Andrew Doran, has replaced her. He has some exciting talks planned for the upcoming year.

A development that we are very excited about is the online availability of current *Madroño* articles. *Madroño* will be available through BIOONE, as well as individually to members via a password. We have kept the cost low for online access to articles to non-members, in order to increase exposure to *Madroño*.

Our Annual Banquet will be held February 23, 2008 at the University of California Santa Cruz Arboretum, in Santa Cruz, CA. Daniel Harder, Director of the Arboretum, will be the second Vice-President in charge of planning the banquet. Our speaker will be John N. Thompson of the Department of Ecology & Evolutionary Biology, University of California, Santa Cruz. This is an outstanding botanical garden to visit in February, and we plan to have a tour of the gardens before the banquet. Mark your calendars now to reserve this date.

Finally, thanks again to all of you for your continued support of our Society. I look forward to seeing you all in February at the banquet, if not sooner!

Dean G. Kelch
October 2007

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EDITOR'S REPORT FOR VOLUME 54

I am pleased to report not only that the California Botanical Society has published another volume of *Madroño*, but that more manuscripts were submitted than during previous years, and that as described in the President's report, *Madroño* articles will now be available online through BioOne.

During the past twelve months, 57 manuscripts were submitted (which is up from 42 during the preceding 12 months). Based on reviews, I requested minor to moderate revisions to 33 manuscripts, major revisions to 9 manuscripts, and rejected 3 manuscripts. (Twelve manuscripts are still in review.) Of those accepted with minor revisions, 18 were published in this volume. The typical interval from submission to publication has remained approximately one year long. During the past two years, this interval has lengthened, in part because of special issues delaying the publication of other manuscripts. However, because no special issues are planned for the coming year, the interval from submission to publication should decrease in the coming year.

During the past twelve months, the number of book reviews and noteworthy collections has also increased. Seven book reviews and 20 noteworthy collections were submitted during the past twelve months (versus 3 and 10, respectively, during the preceding 12 months).

The increase in submittals, together with the distribution of articles through BioOne, bodes well for the quality, breadth, and influence of *Madroño*. And, it indicates the quality, breadth, and quantity of botanical research in western North America.

Authors have been aided by numerous reviewers, an editorial board, Jon Keeley (Book Review Editor), Margriet Wetherwax (Noteworthy Collections Editor), Dieter Wilken (Noteworthy Collections Editor), Steve Timbrook (Index Complier), the Executive Council of the California Botanical Society, and Annielaurie Seifert and her colleagues at Allen Press. Also, Mike Vasey and Jeff Corbin produced Issue 54(3), a special issue on restoration, which was a major contribution. All of these individuals deserve our recognition and thanks for their contributions to *Madroño*.

My term as editor ends with this volume. I thank all of you for the patience and understanding that you showed as I grew into the role of editor, and that you showed during those times when I struggled to keep manuscripts flowing through review, revision, and publication. Helping distribute research to the botanical community has been very fulfilling, and I appreciate the California Botanical Society having given me this opportunity to help out. I also appreciate having been supported by Jean Sheppard, Ellen Dean, and the Department of Plant Sciences at the University of California Davis; EDAW|AECOM; and most of all by my wife Gabrielle and my son Weston.

Professor Paula Schiffman (of California State University, Northridge) is our in-coming editor. Her experience and interests, which range from evolutionary biology and phytogeography to community ecology and conservation, fit well with the scope of our journal, and we are very pleased that she will be editor-in-chief of *Madroño* for the next three years.

John C. Hunter
October 2007

REVIEWERS OF MADROÑO MANUSCRIPTS 2007

Lynn Alder
Barbara Allen-Diaz
Kelly Allred
Ishan Al-Shehbaz
Michael Baad
Donovan Bailey
Bruce Baldwin
Peter Ball
Jim Baxter
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Mark Borchert
Jeffrey Brasher
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Matt Busse
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Classified entries: major subjects, key words, and results; botanical names (new names are in **boldface**); geographical areas; reviews, commentaries. Incidental references to taxa (including most lists and tables) are not indexed separately. Species appearing in Noteworthy Collections are indexed under name, family, and state or country. Authors and titles are listed alphabetically by author in the Table of Contents to the volume.

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DEDICATION

Sherwin Carlquist, world-renowned plant anatomist, island biologist, and systematist, has been an amazingly creative and productive contributor to botany throughout his adult life. A native Californian, Sherwin has enriched the western American botanical community in part through his highly integrative research at Rancho Santa Ana Botanic Garden and, since "retirement" in 1993, at the Santa Barbara Botanic Garden. He also played a major role in scientific education through his dynamic teaching of undergraduates at Pomona College and his mentorship at Claremont Graduate University of many M.A. and Ph.D. students, who in turn went on to distinguished careers in botany. He continues to interact regularly with students in and out of the classroom as an adjunct professor at University of California Santa Barbara.

The worldwide scope of Sherwin's work has included numerous studies that have enhanced understanding of the evolution, ecology, and functional biology of a wide diversity of western American plants, often drawing from detailed anatomical observations. His early studies of islands led to publication of three books (*Island Life*, *Island Biology*, and *Hawaii: A Natural History*) that focused attention on the importance of long-distance dispersal and insular evolution in shaping both mainland and island floras, including the flora of the California Islands. His vast and still growing contribution to plant anatomy, represented in part by hundreds of journal articles, includes three books (*Comparative Plant Anatomy*, *Ecological Strategies of Xylem Evolution*, and *Comparative Wood Anatomy*) that have been highly influential in the continuing synthesis of plant anatomy with evolutionary biology, ecology, and physiology. His books and other writings have inspired generations of scientists and have continued to have that effect long after initial publication.

Over the course of his professional life, Sherwin proposed many daring hypotheses on anatomy, dispersal, and diversification that contradicted then-prevailing wisdom but were subsequently corroborated, as technical advances allowed for additional testing of those ideas. For example, his ideas on xylem evolution, including evolution of woody growth-forms from an ancestrally herbaceous state, challenged entrenched beliefs in the conservatism of wood anatomy. His championing of the importance of long-distance dispersal in the development of both island and mainland biotas was opposed for decades by vicariance biogeographers. His hypothesis that the Californian tarweeds (Madiinae, Compositae) gave rise to the Hawaiian silversword alliance (*Argyroxiphium*, *Dubautia*, and *Wilkesia*), although convincingly demonstrated by his anatomical evidence, directly contradicted contemporary expert opinion. His case for diversification of shrubby tarweeds (*Deinandra*) in the California Islands stood in contrast to the dominant view that woody endemics of the islands of southern California and Baja California are strictly relicts that once occurred on the North American mainland. In all of the above instances, and in too many others to mention

here, Sherwin's hypotheses prevailed and often helped to initiate new lines of research.

At a symposium held in his honor at the 2007 Botanical Society of America meeting in Chicago, Sherwin told young members of the audience not to shy away from publishing and defending controversial hypotheses if they are convinced by careful work that current ideas are flawed. At that meeting and in Chico, California, the previous year (at Botany 2006), Sherwin's concern for the latest generation of scientists was also expressed at two lunchtime sessions that he organized to provide advice and council on career opportunities, research strategies, academic survival, and other daunting considerations for students and postdoctoral researchers. Those activities are in keeping with his oft-stated definition of success as a scientist — to inspire others to carry forward with new, creative work that further advances understanding. In recognition of that spirit of devotion to the future of science and scientists and of his exceptional contributions to botany, the California Botanical Society dedicates this volume of *Madroño* to Sherwin Carlquist.

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